ANIMAL LIFE
AND
UMAN PROGRESS

ANIMAL LIFE
AND HUMAN PROGRESS

ANIMAL LIFE AND HUMAN PROGRESS

EDITED BY

ARTHUR DENDY, D.Sc., F.R.S.

FELLOW OF KING'S COLLEGE AND PROFESSOR OF ZOOLOGY
IN THE UNIVERSITY OF LONDON

LONDON
CONSTABLE AND COMPANY LTD.
1919

PREFACE

This volume is the outcome of a course of nine public lectures delivered at King's College, London, in the Spring term of the Session 1917–18, under the auspices of the Imperial Studies Committee of the University of London. It was felt to be very desirable at this time to bring before the public in as convincing a manner as possible the claims of Zoological Science to recognition on terms of equality with other departments of learning. It would perhaps be better to urge such claims on behalf of the Science of Biology as a whole, for the distinction between zoological and botanical studies is a very arbitrary one, justifiable only as a matter of convenience and hardly comparable with the distinction between the sister sciences of Chemistry and Physics, though I imagine that the latter also breaks down when investigations are pushed beyond certain more or less well-recognised limits. There is, moreover, a strong tendency at the present day to insist upon the obvious fact that most, if not all, of those activities of living organisms which are open to scientific investigation are capable of analysis into what may be termed chemical and physical factors, and this insistence, often pushed to unreasonable extremes, has undoubtedly tended to depreciate the independent value of the biological sciences in many minds.

In an ideal educational atmosphere it would be regarded

as quite unnecessary, if not actually derogatory, to base the claims of any department of learning mainly, or even largely, upon utilitarian considerations. Knowledge for its own sake is a fine watchword, but those who control the national purse-strings and have to justify their expenditure in the eyes of an exacting and not very far-seeing public, not unnaturally like to be able to show some return which the public is capable of appreciating. The utilitarian aspect of our subject cannot, therefore, be altogether ignored—and indeed it is only right that the vast material resources of the animal kingdom should be fully exploited in the interests of mankind. At the same time it is no less necessary that the eyes of the public should be opened to the value of biological studies from a purely academic and educational point of view, and if our national system of education is to rest upon a broad and firm basis we must insist upon the paramount importance of these subjects—the investigation of which alone renders possible the scientific study of man himself in all his manifold relations.

In arranging the present course it was necessary to secure, as far as possible, an adequate treatment of the subject matter from various points of view, and our lecturers were chosen, not merely on account of their academic distinction, but because each one of them might be expected to have something of first-rate importance to say upon some particular aspect of Zoological Science. The subjects of the different lectures have, therefore, not been selected merely at random, but there is a connection between them all which will be obvious at once to the thoughtful reader.

It may at least be claimed for the lectures that they represent the latest views upon matters with which they deal.

If these views appear in some cases to be subversive of modern biological doctrine it must be remembered that biological thought is progressive; were it otherwise the claims of biological science to a foremost place in our educational system might well be considered questionable. The doctrine of Organic Evolution, for example, looms large in several of the lectures, and a certain advance is to be observed from the position held by Charles Darwin and his immediate followers. The foundations of this doctrine, however, remain unshaken, and it is only the superstructure which has been, perhaps too hastily, erected upon them that is being more or less reconstructed in accordance with recent investigations.

The unexpectedly large audiences which were attracted to the lectures, and the great interest evinced in them at the time of delivery, seem to justify the hope that in their present form they may appeal to an even larger circle.

Our great indebtedness to the distinguished men of Science who collaborated in the lecture-course has already been expressed, but I may be pardoned for once more thanking them in my capacity as Editor for the great trouble which they have taken to make this volume a success. I must also express my gratitude to Miss Margaret Tribe, M.Sc., of King's College, for the care and skill with which she has compiled the Index.

ARTHUR DENDY.

King's College, London,
October 1918.

CONTENTS

		PAGE
I.	MAN'S ACCOUNT WITH THE LOWER ANIMALS. By ARTHUR DENDY, D.Sc., F.R.S., Professor of Zoology in the University of London	1
II.	SOME EDUCATIONAL AND MORAL ASPECTS OF ZOOLOGY. By GILBERT C. BOURNE, M.A., D.Sc., F.R.S., Fellow of Merton College, Oxford, and Linacre Professor of Zoology and Comparative Anatomy	23
III.	MUSEUMS AND RESEARCH. By C. TATE REGAN, M.A., F.R.S., of the British Museum (Natural History)	63
IV.	MAN AND THE WEB OF LIFE. By J. ARTHUR THOMSON, M.A., LL.D., Professor of Zoology in the University of Aberdeen	81
V.	THE ORIGIN OF MAN. By F. WOOD JONES, M.B., D.Sc., Professor of Anatomy in the University of London	99
VI.	SOME INHABITANTS OF MAN AND THEIR MIGRATIONS. By R. T. LEIPER, M.D., D.Sc., Reader in Helminthology in the University of London	133
VII.	THE FUTURE OF THE SCIENCE OF BREEDING. By R. C. PUNNETT, M.A., F.R.S., Arthur Balfour Professor of Genetics in the University of Cambridge	155
VIII.	OUR FOOD FROM THE SEA. By W. A. HERDMAN, LL.D., D.Sc., F.R.S., Professor of Zoology in the University of Liverpool	189
IX.	TSETSE-FLIES AND COLONISATION. By R. NEWSTEAD, M.Sc., F.R.S., Professor of Entomology in the University of Liverpool	207
INDEX		221

I

MAN'S ACCOUNT WITH THE LOWER ANIMALS

By ARTHUR DENDY, D.Sc., F.R.S.
Professor of Zoology in the University of London.

I

MAN'S ACCOUNT WITH THE LOWER ANIMALS

As organiser of this course of lectures on behalf of King's College and of the Imperial Studies Committee of the University of London, it falls to my lot to deliver an introductory discourse. In fulfilling this duty I conceive it to be my first privilege to express our heartfelt appreciation of the generous response which has been accorded to our invitations by distinguished zoologists belonging to other seats of learning—a response far more ready and far more generous than we had any right to expect at a time when every one of us is preoccupied with thoughts and anxieties very incompatible with the successful handling of intellectual problems.

You will have gathered already from the programme which has been issued that our joint purpose is to emphasise and illustrate the importance of zoological science from the point of view of human progress. We no longer need to be instructed, especially in these strenuous times, as to the immense influence, for good or evil, which the chemist and the physicist exercise upon the destinies of mankind, whether their energies be employed in the constructive processes of peace or in the destructive ravages of war. The zoologist can perhaps claim little if any direct share in the conduct of the terrific struggle for existence which is now going on throughout the civilised world, but he can and does, I venture to think, play a great part, not only in the amelioration of the conditions of human life, whether in war or peace, but also in the education of the public with regard to many matters which have a very direct bearing upon the future of the human race.

Mankind, after all, is but the highest branch of the great evolutionary tree of the animal kingdom, and if the study of zoology had done no more than establish this fact, which lies at the very root of human existence, it would have justified its claim to recognition as an essential item in our educational programme. The proper study of mankind is man, but before you can study man with any prospect of success you must study the animal kingdom to which he belongs and of which he is the latest product. In other words, you must study zoology.

It is the infinitely varied relations of mankind with the rest of the animal kingdom—with what we are accustomed to speak of as the lower animals—that will occupy our attention this evening, a subject so vast and complex that we shall be able only to glance at some of its more general aspects, with a brief reference to one or two specific questions, leaving it to the eminent specialists who will address us later on to deal in detail with particular problems of exceptional interest.

In a certain very legitimate sense the interest which mankind takes in the rest of the animal kingdom is of the same nature as the interest which any one of us takes in the past and present members of his family. You may study your surviving relatives from purely sentimental or altruistic motives or for the sake of what you can get out of them, and you may study your family pedigree either for the purpose of impressing your acquaintances with your dignity and importance, or with the much more wholesome object of learning all that can be learnt of the causes which have led up to your present position in the world, and of seeking in the history of the past guidance for the future.

If we confine our attention to the animal kingdom as it exists to-day we realise immediately how completely the struggle for existence has turned in favour of man. The larger animals have been for the most part completely exterminated, while those which remain have been subdued or even enlisted in the service of the dominant type. In no part of the world has man, provided with the weapons which he has

fashioned for himself, any cause to fear either conflict or competition with the larger and apparently more dangerous of his fellow-creatures. Everywhere he makes them the ministers of his wants, and, far from wishing to destroy them, seeks to preserve and improve them in his own interests.

The science of breeding, about which Professor Punnett will speak to us on a future occasion, is teaching us how to direct the course of evolution amongst our domesticated animals—and of course the same applies to plants—in such a way as to render them ever more and more perfectly adapted to our own requirements. The scientific breeder shares in the joys of creation, and the products of his creative skill are no less wonderful and no less distinctive than those which have arisen in what we call a state of nature. Our ever-deepening insight into the laws of heredity enables us to produce our results with increasing rapidity and precision, and it is hardly too much to say that we are beginning to look upon the whole organic world as a storehouse of potentialities which may be realised in whatsoever permutations and combinations we may desire. By appropriate mating of carefully selected individuals we may introduce good features and eliminate bad ones, and so literally build up races of plants or animals to suit our special needs.

In this way man—like other animals, essentially a parasite and beast of prey—furnishes for himself immense supplies of food, immense stores of energy to be utilised in his own advancement to a condition which we may hope will ultimately rise above that of the brute, if it has not done so yet.

How to hasten the advent of this very desirable state of things by the further control and exploitation of the animal kingdom is the great problem which the economic zoologist has set himself to solve, and its solution is to be found not in the study of the higher forms of animal life alone.

In the earlier days of human history the struggle for existence was mainly a struggle for food, in which the competitors were mostly outside the select ring in process of formation by our enterprising ancestors. The fruits of the

earth and the spoils of the chase had at first to be shared with many formidable rivals which have long since disappeared from the scene, but, although the larger competitors have been almost eliminated, mankind has not yet acquired complete mastery of the world's food-supplies. It is in this field that the activities of the zoologist are perhaps most usefully employed at the present time, when the struggle for food is once more resuming its former intensity.

I had hoped that it might have been possible to persuade one of our experts in economic zoology to deal with this part of our theme, and it may be regarded as a tribute to its importance that the zoologist to whom I applied was already so fully occupied with work of national urgency that it was quite impossible for him to accede to my request. I do not profess to be an economic zoologist myself, but in these abnormal times most of us seem to find ourselves attending to other people's business, and it so happens that, in conjunction with several colleagues at King's College and elsewhere, I have spent much of my time for some months past in the investigation of a problem which may serve to illustrate this part of our subject.

The problem to which I refer is the protection of our stores of wheat and other cereals from the depredations of destructive insects, and, although as yet only very partially solved, it presents such a variety of interesting and instructive features that it seems worth while to devote a little time to its consideration this evening. Indeed, it may be taken as a type of one of the largest and most important classes of problems with which the student of applied zoology is confronted, and may be used to illustrate not only the nature of the results which he strives to attain but also the methods which he employs.

The problem is not a new one. In America and in India it has already been attacked with some measure of success, and a fairly extensive literature has grown up around the subject; but in this country comparatively little has as yet been done, while the matter has lately assumed special importance in view of the shortage of our food-supplies and

the necessity of storing grain for long periods in some of the principal countries of production.

Opinions vary much as to the actual amount of the damage caused by grain-weevils—under which term are generally included other grain-beetles as well as the true weevils themselves. Some idea of the magnitude of the loss may, however, be gained from the following figures. The world-crop of wheat for the year 1912 was estimated at between three and four thousand million bushels (Nöel-Paton). In America it has been estimated that damage to the extent of 5 per cent is caused by grain-pests, chiefly weevils. One of the largest shippers of Indian wheat, quoted by Mr. Nöel-Paton, has said, on the other hand, that the average wastage from this cause is about 2½ per cent. There is reason to believe that the latter is a very low estimate, but even at this rate the loss on Indian wheat alone would amount to about nine million bushels annually, representing a value of more than £1,000,000. This would have to be multiplied by at least 10, and probably much more, to give the loss for the entire world. I leave out of account the damage to rice and other cereals, and of course, whenever prolonged storage becomes necessary the weevil problem becomes correspondingly accentuated. In Australia, at the present moment, many million pounds' worth of wheat are stacked, it is to be feared under very unfavourable conditions, awaiting shipment, while it was recently reported in the press that Great Britain and France have undertaken to buy and ship before November 1, 1918, 2,500,000 tons of wheat and other cereals from the Argentine.

A really badly weevilled sample of wheat, such as is often found in a ship's cargo after a long voyage through the tropics, would certainly not be a pleasant sight to the fastidious housewife, but to the zoologist it is a wonderful microcosm, full of interesting inhabitants. The grain appears to be alive with insects, swarming through it and burrowing into it. Several different kinds will probably be present. Some of them are primary pests, feeding directly upon the sound grain, which they rapidly reduce to empty husks ; others are of secondary importance, feeding upon the débris produced by

the activity of the principal actors. Most of these are beetles of various kinds and sizes, but always small.

Perhaps the commonest and most destructive of all the grain-pests are the two weevils, *Calandra oryzae* and *Calandra granaria*, easily distinguished from other beetles by the long snouts characteristic of all the weevil family. *Calandra oryzae* has well-developed wings concealed beneath the horny wing-cases or elytra, but it so rarely uses them that one wonders why they have been preserved, especially as *Calandra granaria*, which has precisely similar habits, seems to get on very well without them. The almost microscopical egg is deposited in a hole made in the surface of the grain by the female insect, and in a few days a tiny grub is hatched which at once bores its way into the interior. Here it feeds and grows into a rather shapeless, pulpy larva, which exhibits very little activity and presently passes into the pupal state. Finally the perfect insect emerges and bores its way out of the hollowed grain to enter upon an active existence of some considerable duration. The entire period of development, from egg to perfect insect, under favourable conditions occupies from three weeks to a month. In one of my own experiments the number of adult weevils (*Calandra oryzae*) increased more than three-and-a-half times in less than five weeks at a temperature of about 31° C., the Indian summer temperature. Assuming a threefold increase per month it is easy to calculate that in six months the number of weevils would increase 729 times, and as the adults are rather long-lived and feed voraciously on fresh grains, it is obvious that an enormous amount of damage can be done in the space of a few months.[1]

Of only less importance, apparently, is the small grain-beetle known as *Rhizopertha dominica*. The habits of this insect are very similar to those of the two weevils, but the egg is deposited outside the grain and the young larva has to depend for its food-supply upon the soft frass and damaged grains due to the activities of the parents. In fact the adult insect

[1] In an experiment made since this lecture was delivered a single pair of *Calandra oryzae* gave 1501 adult weevils in 111 days, at a temperature of 25°-28° C. in a moist atmosphere—a multiplication of 750 times.

in boring into the grains produces much larger quantities of flour than it consumes, and the surplus is used by the larvae until they manage to make their way into some grain and begin milling operations on their own account.

A very different species, though again a beetle, is *Trogoderma khapra*. The perfect insect somewhat resembles a small ladybird and is a harmless little creature which apparently need not feed at all; at any rate it does not attack sound grain and is very short-lived. The larva, on the other hand, is one of the most serious of the grain-pests in India, and extreme care ought to be taken that it is not accidentally introduced into other countries warm enough to enable it to thrive. It is so different from the other grain-pests in appearance that it has received a special name from the Indian natives, who speak of it as *khapra*, while all the different kinds of adult beetles seem to be lumped together under the term *susri* (Barnes and Grove). The larvae are characteristically hairy and lead an active life, moving about between the grains and attacking them by gnawing the surface. Their cast skins accumulate in immense numbers on the surface of the grain and soon indicate the presence of the pest.

Of the secondary grain-pests, which do not attack whole grains but feed upon the detritus produced by the activity of other insects, the commonest are perhaps the red flour-beetle (*Tribolium castaneum*), the saw-toothed beetle (*Silvanus surinamensis*) and species of *Laemophloeus*. These are all very easily cultivated in jars of broken wheat and form very convenient subjects of study for those who are interested in insect life-histories. They increase at an enormous rate and under favourable conditions the jars are soon teeming with the worm-like larvae in all stages of development, together with pupae and perfect insects. They seem to be incapable of maintaining themselves in sound wheat and all should probably be regarded as flour-beetles rather than as true grain-beetles.

In many of my cultures large numbers of very beautiful, minute, winged, fly-like insects make their appearance. These are hymenopterous species related to the ants, bees and

wasps. They belong in part to a family known as the *Chalcidae*, which are characteristic parasites of other insects, laying their eggs in the bodies of their victims at various stages of their life-history. The chalcids are very wonderful creatures, exhibiting the most marvellous instincts in the selection of the appropriate places in which to deposit their eggs. Those which occur in grain feed upon the larvae of the beetles, but very little is known about them and this is a field of research which it is hoped will be explored in the near future. The fact that over 5000 species of chalcid parasites have already been described from various sources may serve to give some idea of the enormous extent of the ground that has to be covered by zoological investigation.

Nor are these the only insects that occur in stored cereals, for various small moths and their larvae frequently make their appearance, and genuine bugs are occasionally met with. Little is known of the latter, but they probably feed as parasites upon the larvae of other forms. As a matter of fact, even the notorious bed-bug appears to be really a very well-meaning little creature from the human point of view, and it is only quite by accident that it makes itself objectionable to mankind. It finds its natural food in the larvae of the boring beetles which infest old furniture, with which it is said to have been introduced into this country in the reign of Queen Elizabeth.

In addition to the true insects badly infested samples of grain may also contain enormous numbers of microscopic mites. Some of these closely resemble the common cheese-mite, while others are very curious little creatures which again live as parasites upon the larvae of the grain-insects.

If you wish to gain the upper hand in dealing with your enemy it is always advisable to get to know as much about him and his habits as possible, for you never know where a weak spot in his defences may reveal itself. A problem like that of the grain-pests has to be studied from every point of view in the hope of finding a remedy. We want to know all about the life-histories of the insects we are attacking in order to ascertain whether any one stage is more vulnerable than another, and at what period it is most desirable to apply

preventive or remedial measures. We want to know all about the circumstances under which the insects can thrive, with a view to storing our grain under conditions which make insect life impossible. We want to know what poisons can be applied without injuring the grain for our own purposes. We also want to learn as much as we can about the natural enemies of the grain-pests, especially the hymenopterous parasites to which I have referred, with a view to enlisting them, if possible, in our service.

There is a great variety of problems here, not only for the zoologist but also for the chemist and the physicist acting in co-operation with him. Some of them have already been more or less satisfactorily solved. We know pretty well the limits of temperature within which grain-insects can thrive. We know that they do not like cold and also that by heating the grain to quite a moderate degree they may easily be exterminated. The best method of applying the heat is a problem for the engineer, but it is successfully done in America on a large scale, especially in mills, where it appears to be supplanting the older methods of fumigation by means of carbon bi-sulphide or other poisonous gases. We also know that a certain degree of moisture in the grain is highly favourable to the development of the pests, and that it is therefore necessary that grain intended for storage should be sufficiently well dried.

All this is common knowledge and need not detain us. I had intended, however, to give you an account of some experiments which I myself have lately been making in this connection and which have yielded some rather surprising and interesting results, possibly of considerable practical importance. Unfortunately I am advised that it may be desirable to withhold publication of these results for the time being, and therefore, much as I should like to take you into my confidence, I am afraid that I must not do so.

Illustrations of the economic importance of zoological investigations, analogous to the case which we have just been considering, might be multiplied a thousandfold. I need only

call to mind the important researches of my friend Mr. Durrant, of the Natural History Museum, on the destruction of army biscuits by the flour-moth, *Ephestia kuehniella*, which have proved of great service to the nation and which redound to the credit of an institution the importance of which our present Government seems singularly incapable of appreciating, but which I am sure will be estimated at its true value by my colleague, Mr. Tate Regan, when he comes to speak to us on museums and research. I would also remind you of the far-reaching benefits conferred upon agriculture by the study of the life-histories and habits of innumerable destructive insects which work havoc amongst our growing crops, such as the much-dreaded potato-beetle, the turnip-fly and the codlin-moth. The significance of these problems has long been recognised in the appointment of Government entomologists in all the civilised countries of the world.

No less importance must be attached to the study of those amongst the lower animals which earn their livelihood as parasites upon domesticated animals or upon man himself, having carried the war into the enemy's country in a very literal sense. These may be minor horrors, to use the apt expression of Dr. Shipley, but the sum-total of the loss and suffering which they cause is incalculable. Fortunately, although most of us regard such creatures as fleas, bugs, lice and tapeworms with a not unnatural loathing and contempt, they have a deep intrinsic interest for the zoologist and offer fascinating subjects for scientific investigation. The life-history of even a tapeworm is a veritable romance in low life, full of exciting adventures, cunning contrivances and hair-breadth escapes, and although we may regard the tapeworm as the villain of the piece we can hardly avoid extending a certain amount of sympathy to him in his struggles with adversity. But this is a part of our subject which I can safely leave in the hands of Dr. Leiper and Professor Newstead, who will speak with the authority of specialists on some of the most interesting of human parasites. Suffice it to say here that the science of medicine is every year more and more

indebted to the services of the zoologist, as witnessed by the recent remarkable development of our knowledge of the lowest forms of animal parasites, belonging to that great group of microscopic organisms known as the Protozoa, such as the malaria parasites, the trypanosome of sleeping sickness and the amoeba of dysentery—the importance of which is so great as to have led to the recognition of a separate branch of semi-medical study, to which the somewhat unfortunate name Protozoology has been applied.

Equally important, again, from the utilitarian standpoint, is the study of the marine fauna of the world, regarded chiefly, though by no means entirely, as a source of human food. The great problem of our fisheries will be dealt with by Professor Herdman, though he would be the first to tell you that it is quite impossible to do justice to it within the compass of a single lecture. An international organisation now exists in Europe for the control of our fisheries, and an enormous amount of research is devoted to the problem of maintaining and improving our fish-supplies. I need hardly point out that here again it is the work of the scientific zoologist, especially in the study of the habits and life-histories, not only of the fish themselves but also of the innumerable organisms upon which they feed, that forms the indispensable foundation of all future progress.

I must ask you to turn now to another aspect of our subject. What is it that, above all else, distinguishes a living organism from the inanimate objects by which it is surrounded and which therefore constitute the greater part of its environment? It is the power of reacting towards that environment in such a manner as to conduce to its own well-being; of controlling, not only its own behaviour but also the behaviour alike of its fellow-creatures and of inanimate objects, in its own interests, and thereby maintaining its own position in the universal struggle for existence. The humblest organism exercises some control of this kind. A living bath-sponge, in

its native element, regulates, by means of a beautiful mechanism, the stream of water which circulates through the elaborate system of canals by which it is penetrated, bringing the necessary supply of food and carrying away the waste products. Even the amoeba, the commonly accepted type of primitive simplicity, has the power of selecting those objects which are suitable for food and rejecting those which are not, and if it cannot control its environment to any greater extent it can at least remove itself from injurious influences and seek out the most favourable conditions for its existence.

But this is not all; were it so it would be difficult indeed to explain the fact that living organisms as a whole are constantly undergoing a slow, progressive evolution. From generation to generation the progress is slight and for the most part imperceptible, but in the long-run it has led to the development of the most highly organised animals, even of man himself, from the simplest beginnings, far simpler even than the humble amoeba. This progressive evolution must be attributed largely to the fact that all living organisms, even the lowest, have the remarkable power of learning by experience, of profiting by their mistakes and successes and doing better next time.

The development of a complex animal from the unicellular egg to the perfect individual, with all its marvellous mechanism and potentialities, is only possible because it is based upon the accumulated experience of a long chain of ancestors. How that experience is handed on from generation to generation is a question into which we cannot enter in this place. It is the great problem of heredity, the most debated problem in the whole realm of biological science.

We do not question the value of experience in our own lives. We know well enough that by experience we learn to perform the most complex actions with ever-increasing facility and precision. It is perhaps not generally realised, however, that the living organism actually builds up its own body by its own activities. The first action of the developing egg is to divide itself into daughter-cells, as its ancestors learnt to do when they were unicellular Protozoa, and these daughter-cells gradually multiply and differentiate themselves and combine

together to form tissues and organs, until the entire structure is perfected. All this is done unconsciously, but it is none the less the result of past experience on the part of innumerable antecedent generations of living organisms, each one treading in the path well worn by its predecessors and perhaps making a little progress on its own account.

How far what we call intelligence can be said to be involved in these unconscious processes of growth and development I must leave to students of philosophy to decide, but, at any rate amongst the higher animals, a point is reached in the course of development where the part played by intelligence can no longer be called in question, and in man especially experience is consciously utilised as the most important factor in both individual and racial progress. It is this conscious use of experience that chiefly distinguishes mankind from the lower animals, and the point which I wish to emphasise here is that man, by virtue of his greater intelligence, is able to avail himself not only of the past experience of his own species but of the experience of the entire animal kingdom.

Not the least of the debts which we owe to the lower animals is the liberal education which they offer to those who choose to avail themselves of it, and this education may have a very practical bearing upon human affairs. How many inventions of the human mind have been unconsciously anticipated by the lower animals in the construction of their own bodies? What is the photographic camera but an imperfect imitation of the eye as it occurs in every typical vertebrate? The electric telegraph is little more than an extension, beyond the limits of the body, of the infinitely more perfect system of nerves and ganglia within the body itself. I should not be in the least surprised to learn that something like wireless telegraphy is practised amongst the lower animals, if only we could recognise the apparatus by means of which it is carried on.

The problem of flight has been unconsciously solved no less than four times by different groups of the animal kingdom—insects, reptiles, birds and bats—and by each in

a different way, long before man arrived at a comparatively clumsy solution by the conscious exercise of his intelligence.

There is one little human invention of a very trivial character which always interests me particularly in this connection. Those of us who indulge in the pleasant vice of smoking are familiar with a form of tobacco-tin possessed of two covers. The inner one is hermetically soldered on. The outer one fits on as a lid in the ordinary way, but it is provided with an ingenious little contrivance in the form of a sharp metal point or cutter, capable of being so adjusted that when the lid is twisted round the inner cover is cut through and can be removed. This simple but effective device was anticipated, millions of years ago, by that remarkable animal the tuatara of New Zealand, a creature resembling a large lizard and interesting to the zoologist from many points of view. This animal lays eggs with tough, leathery shells, within which the young tuatara develops until ready to hatch. How is it to get out of the shell? Well, it cuts a slit in it by means of a sharp horny projection developed on the snout, which, having served its purpose in a single action, is never used again and presently disappears.

Those of us who follow the progress of the great war—and who does not?—have lately heard a good deal about "camouflage." The term may be a new one but the idea has been familiar to the zoologist for a great many years. Indeed, human attempts at camouflage are but feeble in comparison with what has been unconsciously accomplished by many of the lower animals. One of the commonest crabs of our own shores nips off pieces of seaweed and dresses itself up in them so as to baffle the pursuit of its voracious enemies. In Australian seas one of those curious fishes, the sea-horses, improves upon this by growing imitation seaweed out of its own skin. Various insects, as is well known, imitate twigs, leaves, or even flowers, with the most artistic fidelity. The cuttle-fish conceals itself on the approach of enemies by discharging a cloud of ink into the water, just as we have recently learnt to protect our ships from enemy attack by means of smoke-clouds.

Something very similar to poison-gas was used by the skunk thousands of years before the Germans ever employed it!

Salmon poachers are said to attract the fish by means of lights exhibited at night. Exactly the same artifice is practised by deep-sea fishes themselves with a view to enticing smaller members of the finny tribe within the range of their rapacious jaws—but in this case the lights are developed as parts of their own bodies, in the form of the so-called phosphorescent organs. In the Malay Archipelago the luminous organs of certain fishes are said to be cut out by the natives and actually used as bait.

I will not weary you with further illustrations, but I may point out that in this direction a vast field still remains to be explored, and many useful lessons no doubt may still be learnt by human inventors. The function of many organs met with amongst various animals is still unknown to us and the study of these may well lead to important developments in applied science. Just as mankind to-day exploits for practical purposes the vast stores of energy laid up in the form of coal by the living plants of past geological epochs, so we may also profit by the no less valuable stores of experience accumulated by the lower animals in the course of their evolution and revealed to us not only in their bodily structure but also in what, for want of a better term, we commonly call their instincts.

But the animal kingdom must not be regarded merely as a kind of technical school for the education of mankind on purely utilitarian lines. In spite of the gross materialism of the present age some of us still rejoice in the possession of an aesthetic faculty and recognise the existence of such a thing as beauty. Some of us even venture to think that the highest function of a university is to foster and develop the aesthetic side of human nature and to cultivate knowledge of all kinds for the sake of what it brings to us in the shape of pure intellectual and aesthetic pleasure, apart altogether from the sordid consideration of whether or not the value of such knowledge is capable of being expressed in terms of bread and butter, or even of motor cars.

That remarkable man, Erasmus Darwin, grandfather of the great prophet of evolution, was fond of giving poetical expression to the delight which he derived from the study of the vegetable kingdom. I suppose, however, that his "Botanic Garden" can hardly be described as classical poetry, and it would certainly take a far greater poet than he to do justice to the feelings which the study of even the lower animals inspires in the mind of the devoted naturalist. The great drawback of scientific zoology is that it leaves all this wealth of beauty out of account. But perhaps, after all, it is well that this should be so, for any attempt to appreciate it in scientific language could but result in lamentable failure. How could any scientific description of a humming-bird, for example, or of a peacock displaying its gorgeous plumage in the sunlight, give any adequate idea of the glorious thing that a humming-bird or a peacock really is? How could any mere scientific treatment do justice to the pleasure which the naturalist derives from the contemplation of the marvellous forms of animal life brought up from the depths of the sea or revealed by the microscope even in the water of a muddy pond?

Whence do we derive our aesthetic sense? Is it some heaven-sent faculty granted to man alone or do we share it with our less-gifted fellow-creatures? Does an insect, as it hovers about the flowers in search of honey, derive any aesthetic satisfaction from their beauty of form and colour or from their fragrance? It surely must do so, for there is the strongest reason for believing that these marvellous forms and colours and scents, which we ourselves appreciate so highly, have arisen in the course of evolution in response to what we may fairly call the tastes of the insects, long before man appeared upon the scene; that they are so many inducements offered to the insects to attract them to the flowers and thereby secure the fertilisation upon which the continued existence of the plants depends. If this be so, what do we ourselves owe to the insects? Have they not set the standard of taste in these matters and are we not their debtors for much of our own aesthetic education and enjoyment? If we lived in a world

where there were no lower animals and no flowers we may be sure that our ideas of beauty would be very different from what they are.

But if scientific zoology altogether fails to do justice to the aesthetic value of the objects with which it deals it nevertheless serves to enhance the delight which we take in them. The beauty of a flower or of a bird's feather may be recognised to some extent by any fashionable or unfashionable lady who uses it for her personal adornment, but what is the pleasure which she derives from it in comparison with that of the student who knows something of its structure and origin and can give an intelligent account of those attributes which render it delightful in our eyes? It is a common saying that familiarity breeds contempt, but I can assure you that the more familiar we become with plants and animals, however lowly they may be, the less inclined do we feel to despise them.

You will remember what Tennyson, who perhaps had a deeper insight into the secrets of nature than any other poet, says on this subject:—

> Flower in the crannied wall,
> I pluck you out of the crannies,
> I hold you here, root and all, in my hand,
> Little flower—but *if* I could understand
> What you are, root and all, and all in all,
> I should know what God and man is.

I leave it to my colleague, Professor Bourne, to deal more adequately with the educational value of zoology, and will only ask you now to consider for a moment what zoological science may have to suggest to us with regard to the future prospects of the human race.

There is, I have been told, a kind of pilgrimage which consists in moving alternately two steps forward and one step back, which must be an extremely irritating method of locomotion. This is the kind of progress which the animal kingdom makes in its journey onwards and upwards through the ages. Higher branches of the great evolutionary tree spring from lower ones, but always from near the base and

never from the apex. The amphibians arose from primitive ancestral fishes and not from such highly specialised fishes as are common at the present day. In the same way the reptiles arose from primitive amphibia and the birds and mammals from primitive reptiles.

Professor Wood Jones will lecture to us on the origin of man and I think he will agree with me that man himself arose from some primitive, unspecialised mammalian stock. Indeed, in his bodily organisation, man still shows many very primitive features, and it is only by virtue of his remarkable brain development that he has been enabled to claim precedence over all the lower animals.

Now the past history of the animal kingdom demonstrates very clearly that over-specialisation in any direction leads, sooner or later, to destruction, and then the running is taken up, so to speak, by some less specialised offshoot of the dominant branch.

Those sinister monsters of the past, the gigantic reptiles which flourished during the secondary period of the earth's history, exhausted their potentialities in the development of brute strength and bodily armour on an enormous scale, together with the huge motor mechanism of bone and muscle necessitated thereby. At the same time their brains were of quite insignificant dimensions, in some cases no thicker than the spinal cord. We have recently been asked, in a sensational advertisement issued in response to a request from the chairman of the War Savings Committee, "How did man conquer the Dinosaurus ?" The question, of course, is an absurd one, for the last dinosaur had become extinct many millions of years before the advent of man. The dinosaurs succumbed to their excessive development of pure brutishness, unleavened by any gleam of intelligence. Man, on the other hand, thinks to find salvation in his brain-power. But are we not, at the present moment, doing exactly the same thing as the dinosaurs and other failures of the past, only consciously and with our eyes open ? It is true we no longer depend exclusively upon our own bodily organisation for our machinery of warfare. Our highly developed intelligence

places all the resources of the earth at our disposal, but the result is likely to be just the same. The struggle for existence is only so much the keener and more deadly.

The curse of mankind to-day is still brutal mechanism, uncontrolled—or very imperfectly controlled—by any higher faculty. Have we already gone too far in this direction, or is it still possible to save our present civilisation, perhaps by a more rational system of education and the consequent development of higher ideals? This is the greatest of all the problems which will have to be solved when the war is over, and it is obvious that it can only be solved by common agreement between all the nations, for so long as one nation insists upon devoting a large part of its resources to armaments, others must do the same in self-defence.

If, however, we are coming to the end of our tether what will take our place? Judging by past experience, it will be some unspecialised offshoot of the human race itself, which will begin once more in a comparatively humble fashion and, with infinite toil and pains, build up a new civilisation and finally reach a level a little higher than that attained by its predecessors.

It is safe to prophesy, for none of us will be here to see whether or not the prophecy is fulfilled—at least we may hope not.

II

SOME EDUCATIONAL AND MORAL ASPECTS OF ZOOLOGY

By GILBERT C. BOURNE, M.A., D.Sc., F.R.S.
Fellow of Merton College, Oxford, and Linacre Professor of Zoology and Comparative Anatomy.

II

SOME EDUCATIONAL AND MORAL ASPECTS OF ZOOLOGY

As I have found it impossible, during the past three years, to take up any magazine or any newly published book that does not deal directly or indirectly with the war, so I have found it impossible, even when dealing with so abstract and peaceful a subject as zoology, to avoid looking at it in its relation to the events going on around us.

Nor do I think that I need apologise for doing so. At a time when deeply rooted institutions, systems of politics, beliefs which form the basis of modern civilisation, are put on their trial and required to justify their existence, it is a proper thing to try to give some account of the tendencies of a branch of learning to which I, in common with a number of people, have devoted the whole or a larger part of my life's work. I propose, therefore, to consider in outline what the science of zoology has done for the good of mankind :—what influence its teaching had before the war : what part, if any, it has filled during the war : what *usefulness*—I use the word deliberately—it is likely to have after the war.

In war itself zoology has not taken a conspicuous part. Its value, as assessed by politicians, may be gauged by the treatment proposed to be meted out to the Natural History Museum at South Kensington, and by the sublime ignorance of the value and interest of zoological collections shown by a Government Department. And I observe that zoological teachers and professors, when past military age, are mostly pursuing their normal course of work undisturbed. Their

services, though freely offered, are not considered specially useful in war.

In this zoology differs much from the non-biological sciences; from chemistry and physics in particular. *They* have been harnessed to the chariot of Mars, and have been responsible for much of the horror and destructiveness of modern warfare. High explosives, poison gas, flame-projectors, aeroplanes and Zeppelins, submarines, are all of them contributions of chemical and physical science to warfare.

But, so far as I know, zoology stands acquitted of all responsibility in this respect; it has not supplied any engine for the destruction of human life.

On the contrary, it may justly lay claim to have unobtrusively done much to mitigate suffering and to diminish loss of life. For it is primarily because, in past years, zoologists have not thought it beneath their dignity to devote their lives to the study of the most insignificant forms of animals, that the loss of life through sickness and disease has been so immeasurably less in this than in any previous war. The credit goes to pathology and preventive medicine, and they richly deserve it, but none the less they could not have done all that they have if it had not been for the labours of zoologists.

For the rest the aid of zoology has been invoked, but very slightly in comparison with the sister science of botany, in the production of food; in giving advice on the breeding of domestic animals; in teaching how to recognise and destroy insect and other animal pests; and, in a very small way, in advice on the subject of fisheries.

It is something to be able to claim for the science that one professes that, in a time of savagery, its influence has been altogether benign. But I am not clear that zoology can be acquitted of a malign influence in the years preceding the outbreak of the war.

In this country, where the Government, and the great British public itself, are magnificently impervious to academical teaching, and where, before the war, any public statement on the part of a body of professors was a signal for an

outburst of derision, abstract biological doctrines had very little weight.

But in Germany, where learning is pressed into the service of the Government, and where a section of the Professoriate (but I am glad to say by no means all) trim their sails to catch a favouring bureaucratic breeze, the doctrine of the Struggle for Existence and the Survival of the Fittest has been claimed as a sanction not only for unlimited commercial competition, but for military aggression; for ruthlessness in every form; for world domination; in short, for all that we are now fighting against. The possibility of this application of the Darwinian theory to human affairs was not unrecognised in this country. It formed the subject of many essays some twenty-five or thirty years ago, and was, no doubt, responsible for much of the aversion to Darwin's teaching, and for its slow acceptance even among the educated classes in Great Britain. But this aspect of zoological theory became a cult among the ultra-patriotic Germans. The writings of Strauss, now more than forty years old, are probably forgotten, but the more recent works of Bernhardi and other authors, scarcely known in England before 1914, are sufficient to assure us that for a long time the German people has been taught that war is a holy thing because *natural*, that it is a necessary consequence of "the great biological law," and that nothing but failure and contempt are reserved for those who would inaugurate a reign of peace or suggest any other social order than that of unrestricted competition.

"*Destroy thy neighbour, that thy days may be long in the land which the struggle for existence giveth thee.*" That would seem to be the creed founded on what I hold to be a misrepresentation or at least a misapplication of the evolutionary theory.

Partly because of the humble and pacific part that it has played in the past three-and-a-half years, partly because of this bellicose application of one of its doctrines, it is to be feared that zoology will start with a handicap in the reconstruction that is to follow after the war.

A large part of this reconstruction is to be educational.

There are schemes afoot for speeding up the teaching of many subjects. Languages, geography, history, chemistry, engineering, agriculture, are to be studied with an intensity hitherto unknown in this country, with the avowed object of maintaining our commercial supremacy in the greatly increased competition with the rest of the world that is anticipated in the future. Incidentally, this supremacy is to put us beyond reach of rivalry and so to repair and restore our wealth that we may face the expense of another war with equanimity. That this is the intention of a considerable class of politicians and publicists may be gathered from their speeches, writings and activities. From such, zoologists may expect but little sympathy. It was they who before the war, and long before, were wont to ask of us, "What is the use of your zoology? What does it do for us? Can you make money out of it, or power, or political influence?" These are the Philistines of Matthew Arnold. The Philistines were a warlike nation, and crass utilitarianism is one of the products of war.

But there is another scheme of social reconstruction, previously identified with pacifism and socialism and other dreaded "isms," but now coming rapidly to the front and asserting itself with no uncertain voice. This has as its main objects the abolition of militarism in any form, the elimination of competition, and the recognition of the equality both of nations and individuals.

This school of thought is hostile to zoological doctrine, because, as its adherents have learnt from the German military publicists, and as they had begun to suspect some time before the war broke out, it is possible to use it as an argument against many of their most cherished beliefs.

Whichever of these two conflicting schools of ideas prevails, it would seem that zoological science must start with the handicap of apathy or suspicion.

It is my belief, and I am going to try to justify it, that the science of zoology has a high educational and moral value, and that it would be calamitous if its teaching were neglected,

either by educationists or moralists, in the reconstruction that we hope we may soon be actively engaged on.

I am not going to try to defend its study on utilitarian grounds. That it has a certain utilitarian value is obvious. Many of the diseases from which we suffer, much of the loss sustained by our crops and domestic animals, are caused by animal parasites; and unless we are able to identify with certainty and to follow up accurately the habits of these pests we cannot hope to mitigate them. In connection with the improvement of our breeds of cattle and other domestic animals the study of genetics, common to zoology and botany, has made vast strides in recent years, and when peace allows these biological studies to be resumed, still greater results may be expected. It is not necessary to labour this point any further.

But, apart from its inherent interest and its value as a source of intellectual pleasure, zoology has a special claim on our attention because of its *usefulness* as a training of our faculties and as a guide, and no uncertain guide, in our aspirations towards higher ideals of human welfare and improvement in social organisation.

Here let me say that I use the term zoology in exactly the same sense as Huxley used it fifty-six years ago, as "denoting the whole doctrine of animal life, in contradistinction to botany, which signifies the whole doctrine of vegetable life."

This wide scope of zoology was summed up, in an aphoristic manner, by Linnaeus when he wrote: "Lapides crescunt; vegetabilia crescunt et vivunt; animalia crescunt, vivunt et sentiunt."

"Animalia . . . sentiunt!" These two words express the great difference between the subject matter of zoology and that of all the other natural sciences. Animals feel, and therefore are akin to ourselves. The relationship is insistent. One realises its importance at every recurrent period when one begins afresh a course of instruction in elementary zoology. Without exception one's students ask, "How does all this that you tell us about animals stand in relation to ourselves?" The obvious analogy between man and the higher animals, in structure, in

development, in habits, in instincts, passions and emotions, has been recognised since the dawn of reason, and is to-day recognised perhaps even more clearly by savages than by civilised races. But that man is included in the animal series, has been evolved from non-human animal forms, and retains many psychical as well as structural evidences of that descent, was a doctrine for a long time repugnant to the majority of thinking persons.

Fifty years ago it required great energy and still more courage on the part of Darwin, Huxley, Lyall, Haeckel, Carl Vogt and many others, to establish this proposition. And to this day it remains unacceptable to a large number of people. They spare no effort to evade or at least to minimise its significance. "Granted," they say, "that in structure, in the manner of his birth, growth and death, in his bodily functions and in his lower passions and instincts, man is one with the animals, yet in the possession of the faculty of reason, of self-consciousness, and volition, he stands so far apart from all the rest of the animal world that any argument on social or political questions, based on zoological analogy, is altogether worthless."

One may and does readily concede that the analogy must not be pushed too far: that man has powers of self-determination which profoundly modify, if they do not altogether abrogate, the incidence of natural laws to which the rest of the animal world is subject. Nevertheless this concession does not alter the fact that man, in common with all other living things, has a very complex composition, slowly built up in the past; that his whole bodily and mental constitution is, as Weismann expressed it, "historical"; the outcome of all the additions and all the subtractions of his past history; that it is through and by the agency of that constitution that his reason operates and finds its expression; and that, do what he will, he cannot divest himself of it, nor undo the warp and the woof of the fabric that the past has woven.

This, as it seems to me, is a very great and pregnant truth; very necessary to be borne in mind by those who frame ideal schemes for the betterment of the human race.

It is one of the aspects of the doctrine of evolution, that we

have risen from a lower condition, just as these schemes for betterment present another aspect of the same doctrine, namely, that we are capable of rising to a higher condition.

It is because of our belief in the doctrine of evolution that we recognise that man has progressed in the past. We no longer believe that he has degraded from a primitively perfect and semi-divine condition. And it is because of our belief in the efficacy and continuity of evolution that we confidently expect that man is able to progress in the future and to rise to a higher social state than that in which he now is.

Evolution is a biological doctrine, and, in its application to human affairs, a zoological doctrine; for, as I have already indicated, the study of vegetable evolution offers but few points of contact for the student of human sociology.

Need I bring forward any further evidence in support of the proposition that the study of zoology has special usefulness in connection with problems that have to be decided after the war?

Well then, if we are to embark upon courses fraught with every possibility of good and evil for mankind, and are impelled to these courses by a faith in evolution, is it not desirable, is it not necessary, that we should examine the doctrine?

Evolution is for most people a term of vague import, somewhat hazily associated with such catchwords as the "struggle for existence" and the "survival of the fittest."

Actually, in its widest sense, evolution is the statement that nothing stands still; it is the modern rendering of the *πάντα ῥεῖ* of Heracleitus.

The modern doctrine does not assert that there is any tendency towards perfection, towards a divine ideal, as the evolutionists of the eighteenth century taught.

Looked at in its widest aspect, zoology (and no less botany) teach us that the course of evolution has been very complex and very manifold. On the whole, organisation has progressed greatly in complexity, but not in a straight line. We continually find rapid advances along a certain line; then the impetus in this particular direction seems to come to a stop, and a highly specialised race dies out without leaving any successors.

Its place is taken by more lowly members of the stock from which it was originally derived. We see this has happened again and again. One may give as examples the Ammonites which were abundant in later Palaeozoic times, and in the secondary period look as though they were striving to maintain a foothold by ever-increasing elaboration of structure. But they failed and became utterly extinct. The Reptiles underwent an astonishing development in size and adaptation to different modes of existence in the secondary period. They were giants of the land and sea, and must be reckoned among the most formidable animals that the world has ever seen. They became denizens of the air as well as of the sea and land. But all these terrifying monsters with their highly developed protective and aggressive structures died out, and though the class survives in large numbers and variety to the present day, it has lost its former pre-eminence and has had to yield pride of place to two of its offshoots, the birds and mammals.

Numerous, too, are the cases in which there has been no ascent in the scale of organisation, but, contrariwise, a degradation, most obvious in sedentary and parasitic animals. This may go so far that many parasites are reduced to mere sacs, in which all organs of perception, locomotion, respiration and even alimentation have disappeared, and little more is left than the reproductive organs.

On the whole, however, the progress has been forwards and not backwards, though the history of animal evolution teaches us that the battle has not always been to the apparently strong nor the race to the apparently swift. There have been many ups and downs, many failures on the part of organisms that seemed competent to overcome all their contemporaries in a struggle for existence. On the other hand, many quite humble and relatively lowly organised forms have succeeded in surviving with very little change, and flourish to the present day.

Evidently, then, evolution has been a very complex as well as a very slow and uncertain process, and the intricacies of it are not to be mastered by a slight, second-hand acquaintance with zoological theory.

I have been taking the fact of evolution for granted, but really we know little or nothing about it at first hand. It is properly called a *doctrine*; that is, something taught; and in this case the thing taught is a very wide generalisation founded upon evidence culled from comparative anatomy, comparative embryology, palaeontology, geographical distribution and, finally, upon breeding and experiment, all of which are provinces of the great subject of zoology. We believe the doctrine to be true because the evidence derived from all these sources is consistent and points to the same conclusion.

Time forbids my making an attempt to outline the evidence afforded by even one of these sources, but I wish to emphasise the point that, although the doctrine is highly abstract and the product of our reason, the evidence upon which we rely is solid concrete fact, and that the whole edifice of our reasoning would collapse if it could be shown that the facts point to any other conclusion.

Evolution is not a process that we can see going on before our eyes. It is an interpretation of marks that we see everywhere, but it may not be the right interpretation. If we are to accept it, we must be able to represent clearly to our minds the manner and course of evolution and the natural laws governing it. For clearly the marks that we see are the result of the operation of forces which we have to seek out and understand.

As is well known, there were evolutionists long before Darwin, but the theory only found acceptance when he and Wallace gave an intelligible account of the interactions of certain recognised natural phenomena and demonstrated that they gave a credible explanation of the marks in question.

I have avoided using the term natural laws because I am by no means clear that the theory of the evolution of species by the agency of Natural Selection can properly be called a law, that is to say, a statement of invariable sequences.

Using the most general terms, the theory of Natural Selection asserts that progression and regression in the scale of organisation are the outcome of competition among animals for the means of subsistence. If this be absolutely

true, and if it be applicable to human as well as to animal progress, it is a statement fraught with moral consequences of the highest importance.

I cannot do better here than quote the concluding passage from Darwin's *Origin of Species* (he is speaking of the contemplation of a tangled bank, with all its variety of plant and animal life):—

"These elaborately constructed forms, so different from each other, and dependent on each other in so complex a manner, have all been produced by laws acting around us. These laws, taken in the largest sense, being Growth with Reproduction; Inheritance which is almost implied by Reproduction; Variability from the indirect and direct action of the conditions of life, and from use and disuse; a Ratio of Increase so high as to lead to a struggle for Life, and as a consequence to Natural Selection, entailing Divergence of Character and the extinction of less improved forms. Thus from the War of Nature, from famine and death, the most exalted product which we are capable of conceiving, namely the production of the higher animals, directly follows."

It would be difficult to maintain that this passage is not a justification of the German point of view.

The chief criticism of this passage, which was meant to be and is a summary of Darwin's doctrine, must be directed against the application, at the time when the words were written, of the term "laws" to Reproduction, Inheritance and Variability. The truth is that these so-called laws are only phenomena, and that neither Darwin nor his contemporaries knew much about the laws governing any of them.

It is true that Darwin collected and published, in his *Variation of Animals and Plants under Domestication*, a large number of facts bearing on Variation and Heredity, some of which were the outcome of his own elaborate breeding experiments, and he essayed to give an explanation of them in his provisional hypothesis of Pangenesis. So (in point of time rather before him) had Herbert Spencer. And it would be easy, beginning with Aristotle, to cite the names of a large number of philosophers and naturalists—Harvey, Leibnitz,

Buffon, Ch. Bonnet, Oken, Treviranus, Lamarck, only to mention a few of them—who devoted great learning and research to the elucidation of these phenomena. But it cannot be said that any of them got beyond the stage of ingenious hypothesis, and it is to be remembered that Darwin expressly called Pangenesis a provisional hypothesis.

But, though it was unacceptable from the beginning, it proved to be an astonishingly fertile hypothesis. It may claim to have been the parent of the exact statistical researches of Galton and the elaborate, highly technical and very influential theories of Weismann, and of de Vries' Intracellular Pangenesis (1889), not to mention a host of hypotheses less securely founded and now half forgotten.

Quite independent of Darwin's work were the discoveries of Gregor Mendel. He tells us himself that his experiments were begun in the year 1857, the year before Darwin and Wallace read their joint paper before the Linnean Society, and two years before the publication of the *Origin of Species*. The story of how Mendel's work escaped attention and lay practically unknown and forgotten till the year 1900 is now so familiar that I need do no more than allude to it. The wonder of it is, why did not the Abbot of Brünn send a separate copy of his work to Darwin ? Had he done so, I do not doubt that biological science, and I think the world, would have taken a different course. The Abbot cannot altogether be exonerated from the charge of theological prejudice. The work of Darwin was familiar to him ; he is known to have disagreed with Darwin's doctrine, and there seems to have been some aversion to opening up communications.

However this may be, and it is quite a non-essential point, the great and intensive studies of Heredity and Variation that have followed the rediscovery of Mendel's work have gone far to modify some of the cruder conceptions founded on the Darwinian theory.

It is not my purpose to attempt to give you a sketch of or to enter upon a critical examination of any of the theories of the authors whose names I have mentioned. If it were, I should have to ask you to listen to me for many hours, and

probably I should be repeating what is already well known to most of you.

I only propose to state as briefly as possible some of the conclusions of biological science which seem to me so well founded and so incontrovertible that they must be taken into account in all our reasoning and in all our practice regarding living things, particularly living animals, including man himself.

In doing this I may take as a text the quotation that I have read from the concluding passages of the *Origin of Species*, and need hardly go further afield.

In the first sentence there is reference to the dependence of animal (and vegetable) forms on one another. I may amplify this by another quotation (*Origin of Species*, p. 60): "The structure of every organic being is related, in the most essential yet often hidden manner, to that of all other organic beings with which it comes into competition for food or residence, or from which it has to escape or on which it preys."

This is a statement of the universal phenomenon of *adaptation* among living organisms. It is a phenomenon which attracted the attention of the earliest naturalists. As the quotations show, it attracted Darwin's special interest, and it forces itself more and more on our attention as our knowledge of zoology increases.

There is no more fascinating branch of zoology than the study of adaptations; their complexity and the fineness of adjustment displayed by them are marvellous, and it is a point well worthy of remark that delicacy and complexity of adaptation are no less strikingly exemplified in the simplest and most lowly organised animals than in the highest and most complex. An example, now well known, is furnished by the malarial parasites. There are three kinds which produce malaria in human subjects, and their life-history is divided into two cycles:—an agamic cycle, in which the parasite multiplies very rapidly in the human blood; a gamic cycle, followed by production of the so-called sporozoites, which takes place in a mosquito. When an infected female mosquito sucks blood from an uninfected human subject, it injects a number of sporozoites

into the blood of the latter, and so sets up infection. Conversely, when an uninfected mosquito sucks blood from an infected human subject, it sucks up the particular forms of the parasite competent to start the new cycle in the mosquito's body. Thus there is a remarkable adaptation of the parasite to two very different animals, man and a mosquito, and its life-history is correspondingly complex. But that is not all. The same story might be told of birds and a form of mosquito that we usually call the common gnat, *Culex pipiens*; for many birds suffer from a form of malaria, and the mode of transmission and the life-history of the avian parasite are extremely similar to those of the human parasite. But the common gnat, as we all know, sucks human blood. Nevertheless, if infected with bird malaria, it cannot transmit it to man, and if it draws blood from a malarious human subject, all the parasitic stages of human malaria are promptly digested in the gnat's stomach. Human malaria is only communicable by gnats (or mosquitoes) of the sub-family *Anophelinae*, and they are incapable of being infected by and therefore of transmitting avian malaria.

In other words, these two sets of parasites, so similar in appearance, in structure and in mode of existence, are so nicely adjusted to two different pairs of animals that they occupy totally distinct provinces in Nature and cannot exchange places. A quite similar story might be told of the microscopic parasites causing tsetse-fly disease in cattle and sleeping sickness in man, and numerous other examples might be cited. There is a further aspect of the phenomenon. The Anopheline mosquito is so adjusted to the presence of the malarial parasite that it does not seem to suffer any particular inconvenience from its presence. As we say, it is "tolerant" of the parasite. The constitution of the negro is similarly adjusted, and he is tolerant of and suffers no grievous effects from malaria, but the European, as we know well, is not so adapted and suffers accordingly.

We can pass to a much more familiar case of adaptation. As all who collect butterflies and moths and rear up caterpillars know, most caterpillars are attached to a particular

food plant, that is to say are adapted to it, more or less closely, though the amount of dependence of a caterpillar on a particular food plant varies a good deal in different species. Often, however, closely allied species are attached to different plants. Analogous cases might be cited of the Sphegidae, the species of which are attached to particular species of other insects, or spiders, which they store in various ways as food for their grubs.

It would be easy to multiply instances, especially from insects, whose habits have been so closely studied, but those I have given will suffice to illustrate the point I wish to raise. In each of these cases, do not these nearly related forms of animal life withdraw from competition with one another, rather than enter into it?

In every instance the adaptation that we admire enables the organism to occupy some new territory and thus to avoid competition for food or shelter with its nearest relatives. I submit that this aspect of the question has not been sufficiently considered, and that too much stress has been laid upon the competition alleged to take place between individuals of a species and closely related forms. In this connection it is necessary to remember that Darwin derived his conception of the struggle for existence from Malthus, thus applying to the rest of the animal kingdom an idea borrowed from a student of human sociology. It is true that mankind, largely in consequence of the dominion he has gained over the lower animals, has entered into the fiercest competition with his own kind; nation with nation, tribe with tribe, individual with individual. But I am by no means clear that this principle enters, to the extent attributed to it, into the polity of the lower animals. And if it does not, Natural Selection ceases to have the importance attributed to it by Darwin and Wallace; still less the omnipotence (*Allmacht*) claimed for it by Weismann.

To further illustrate this point, I will take the case of Lamellibranchiate (Bivalve) molluscs. They are a very ancient and a very successful group, in the sense that they are numerous in individuals, wide-ranging, and abundant in

genera and species. All have a similar mode of nutrition. They feed on microscopic animals filtered out of the water by the sieve-like apparatus of their gills. Take as a familiar example the common oyster, the life-conditions of which I studied in detail some years ago. It has many *enemies*, chief among them the dog-whelk and the starfish, against which its stout shell is only an insecure protection, but how far can it be said to compete with its own kind? Certainly oyster cannot be said to enter into vigorous competition with oyster, for where enemies are kept in check, as in oyster-beds, the oysters occupy the ground as thickly as they can lie, and flourish and grow fat in this crowded condition, provided, of course, that food-bearing currents are present. Nor do they enter into competition with other lamellibranchs, *e.g.* with mussels, which affect other localities where they can cling to rocks or piles by their byssus, nor yet with pectens, or with cockles or Tapes, Venus, Cythere or other forms with siphons which bury themselves in sand or mud. The only "competitors" that I know of are *Anomia* and the gastropod *Crepidula*. The former, I think, is not so much a competitor as objectionable to the oyster-culturist because it spoils the look of the shells. The latter does appear to be detrimental to oyster-beds when, as in Essex, it increases in such numbers as to smother and crowd out the oysters. It is an importation from America, and an instance of the commonly observed fact that a foreigner tends to upset the equilibrium established among indigenous inhabitants.

In general, lamellibranchs occupy somewhat different localities in the marine territory, and are so adjusted to their particular conditions that they do not interfere with one another. But they are preyed upon by all sorts of other animals and display all sorts of adaptive structural devices to protect themselves from being eaten. These appear to be only partially successful, for there is little doubt that the main protection of any lamellibranch species against extinction by its enemies is its immense fecundity.

Without giving any further examples, which might be multiplied manifold, I submit that too much stress has been

laid upon "competition" by the exponents of the theory of Natural Selection.

A very high authority, Professor Thomas Hunt Morgan, has arrived at practically the same opinion by a very different chain of reasoning. I will quote his words (*A Critique of the Theory of Evolution*, Princeton, 1916, p. 87):—

"Such a view" (I propose to consider his view later on) "gives us a somewhat different picture of the process of evolution from the old idea of a ferocious struggle between the individuals of a species with the survival of the fittest and the annihilation of the less fit. Evolution assumes a more peaceful aspect. New and advantageous characters survive by incorporating themselves into the race, improving it and opening to it new opportunities. In other words, the emphasis may be placed less on the competition between the individuals of a species (because the destruction of the less fit does not *in itself* lead to anything that is new) than on the appearance of new characters and modifications of old characters that become incorporated in the species, for on these depends the evolution of the race."

Let us distinguish, then, between "competition" and "predacity." The "War of Nature," upon which Darwin and his followers lay so much stress, exists, as we all know, and the part it has played in the evolution of animal organisation is clearly of great importance. But it is not fratricidal. There are beasts of prey and beasts preyed upon. To return to my second quotation from the *Origin of Species*, these two sets of creatures "are related in a most essential yet often hidden manner" and have, on the one hand, developed claws, fangs, speed, cunning and strength; on the other hand, protective organs, means of concealment, fleetness, wariness and many other qualities, according to the category to which they belong. Not the least important of the qualities developed by animals that serve as food is fecundity. The species is saved from extinction by its inordinate fertility, and I think it may safely be said that the ratio of increase of a predaceous animal is never so high as that of the animals on which it habitually preys. If it were, it is obvious that the carnivores in every

class of the animal kingdom would soon exhaust the available supply of food and perish by famine.

It follows, from this consideration, that the "Ratio of Increase so high as to lead to a struggle for life and as a consequence to Natural Selection" has not exactly the significance commonly attributed to it. The fishes that swarm in the sea and prey upon one another are subject to destruction at every stage of their existence, and the species only maintain their existence by their fertility. They produce enormous numbers of eggs, which for the most part float on the surface, and afford food for innumerable other animals. These passive embryonic stages cannot be said to enter into competition with one another, yet probably it is at this stage that the rate of destruction is the highest. The newly hatched and defenceless young are again a source of food and a prey to other creatures, and they again can hardly be regarded as actively competing with one another. It is when the highest rate of destruction is past that the survivors begin to develop their adaptive characters, and these promptly lead to segregation of the species, which henceforth live more or less apart, as schools of mackerel, or as the more solitary bottom-frequenting flounders, plaice and Pleuronectids generally. The inference is that a very high ratio of increase is itself an adaptation, having high survival value. This point of view is different from that usually taken up, which assumes that all organisms are striving to increase at the greatest possible rate and that adaptation is the consequence of the increase.

In the essay "On the Duration of Life," which formed the starting-point of his elaborately constructed theories, Weismann clearly brought out the fact that, not only is there a correlation between the length of life and the time and care bestowed on the nurture of their young by animals, but also, the higher instincts and organisation implied by this parental care are associated with a diminished fecundity. Of course the term "Ratio of Increase" may be taken to mean, *not* the actual fecundity, that is to say the power of producing a given number of eggs or young by any animal, but the numbers which survive all the vicissitudes of youth and are able in

their turn to reproduce their kind. This, however, would deprive the term of nearly all meaning in relation to Natural Selection, for on an average of years the numbers of such individuals remain constant in any given species.

I think that we may take it that fecundity is an adaptation preserved by Natural Selection, rather than that adaptations are a consequence of fecundity through the operation of Natural Selection.

Now let us turn to the phenomena of variability and inheritance, so closely bound up with adaptation, and, as Darwin said, "almost implied by reproduction."

Inheritance and variation are familiar facts, the one term expressing our experience that offspring resemble their parents, the other that, inheritance notwithstanding, the offspring never *exactly* resemble their parents.

Defining Natural Selection as the process whereby individuals which display variations giving them ever so small a superiority over their fellows have the best chance of survival, while less happily endowed individuals succumb in the struggle for existence, the theory of Darwin and Wallace asserts that Natural Selection, seizing upon favourable variations, as a breeder selects desirable deviations of structure in his cattle, fixes them by inheritance, and, by a continuance of this process through many generations, is able to accumulate slight variations in a given direction until the most complex organs are produced.

From which arises the corollary that if there is no competition there is no struggle for existence, and if there be no struggle there is no selection of favourable variations, and the race cannot improve.

It is assumed by the adherents of the theory, and Wallace laid special stress on the point, that variations can be accumulated by selection, to almost any desired degree, in a definite direction. The assumption is a necessary part of the theory, for if there is a limit to the amount of variation the power attributed to selection could not exist. Darwin, however, was much more cautious and always much more responsive to sound criticism than Wallace. For reasons that will be

made clear directly, he gradually abandoned his belief in the accumulation of variations by Natural Selection, and laid more stress on the use and disuse of organs and the direct and indirect effects of external conditions in producing variation.

Time is getting short, and it is impossible to give the evidence at length. But I may say at once that it is proved, beyond all doubt, that the small individual variations relied upon by the selection theory are not unlimited.

The late Sir Francis Galton, by the application of exact statistical methods to the study of Heredity and Variation, showed that, with regard to any one character, the range of variability within the limits of a race is confined within certain limits, which may be expressed by a curve of probability. Further, that the offspring of an individual chosen from one extreme of the curve do not inherit to the full the deviation of the parent from the normal, but tend to regress towards the latter. This "law of regression" has been so well established that I need not say any more about it, except to give a striking instance taken from de Vries' famous work on the "Mutation Theory."

As long ago as 1851 the famous Belgian cultivator, Louis Vilmorin, began a long course of improvement of the sugar-contents of the sugar-beet by selection. He found that the saccharine contents of single roots varied from 7 to 14 per cent; and selecting seed only from the best beets, in the second generation had some beets with 21 per cent of sugar. By continued selection of seed from the best beets, aided by greatly improved methods of determining the sugar-contents, he and his followers have been able to raise the average contents to a considerable extent, from 8 per cent to 16 per cent, but this only by a rigorous selection of the best plants in every generation. But they have not succeeded in overstepping the upper limit of variability, namely, 21 per cent, a result obtained in the earliest days of the experiment more than sixty years ago!

All these experiments on beets were undertaken for commercial purposes. I will now give you a famous experiment

by the Danish botanist Johannsen, undertaken for scientific purposes, and with a definite object in view.

Johannsen worked with the common bean, which is self-fertilising, and therefore the difficulties introduced by the mingling of characters in biparental reproduction are eliminated. Beans taken at random from a number of unselected plants were weighed and the results gave a typical curve of probability. Johannsen kept separate the seeds from each plant and sowed them separately. The result was that in the new generation groups were sorted out which had different modes from that of the original population. Some of these groups were similar, some different, and the differences consisted in the average or "median" being different. In some the "median" weight was higher, in some lower than that of the original population, but in each group the seeds varied in weight according to the law of probability. Seeds from each group were sown again and there was no further breaking up into groups. In each group, called by Johannsen a "line," the individuals ranged themselves about the median proper to the line, and this median was the same as in the first filial generation. But in every line there was variation among the individual seeds; some were small, many medium, some large. In further breeding it made no difference whether a small bean or a large bean was chosen for seed, the progeny conformed to the modal curve of the "line" and gave large, medium and small beans, within the modal limits. All of which means that the original population was mixed, and consisted of a number of pure lines, each having its own modality. When these pure lines were sorted out, each showed a limited range of individual variability and bred true to it. In other words, the germinal constitution of each pure line is fixed, and the individual variations occurring within it are due to the varying incidence of external conditions upon identical constitutions. There can be no progression, and also no regression, in a pure line, and selection is powerless to alter it.

But in plants that are not self-fertilising, and in animals in general (for animals are mostly biparental), every union between male and female means the mingling of two

separate germ-plasms, which may be similar, but may be different, in respect of the "factor" in question.

If they are similar, you will get a "pure line" in respect of the particular character that the factor in the germ-plasm evokes. But if they are different, then some of the offspring will have characters produced by the paternal factor, others will have characters produced by the maternal factor, and there will be differences which may affect the well-being of individuals, and consequently give scope to the agency of selection, whether man's selection or Natural Selection.

It was the recognition of this fact that led Weismann to attribute variation to "Amphimixis," by which term he meant the mingling of the germ-plasms of two separate individuals.

I have used the term "germ-plasm." Do you all know exactly what that term means? For the sake of those who may not know, I will try to give a brief explanation.

You all know that an egg is capable of giving rise to a chick. There is an immense difference in structure and in "vitality" (if I may try to compress a large number of phenomena into a single word) between the egg and the chick. A fowl's egg, with its shell, its white and its yolk, is rather a complicated thing. Let us take a simpler, a frog's egg, a little spherical mass, no bigger than a shot. This, under proper conditions, gives rise to a tadpole, and the tadpole grows into a frog. And for still greater simplicity's sake let us take a plant. It is a familiar fact that a flower has to be pollinated or fertilised before it will set seed. Pollen is made up of very minute grains, and leaving certain complications out of account, we may call this the male germ. Deep down in the pistil of the flower is the female germ, a minute single cell. In fertilisation the pollen-grain sends down a tube to the female germ-cell or ovum, and the substance of the pollen (♂) is mingled with the substance of the ovum (♀). The result of this mingling of the substance, or "plasm," of these two is that the plant ovum is stimulated to growth and produces a seed (which is really the quiescent stage of a young plant), and the seed when sown grows into a plant, which in turn

produces flowers, and the whole process is repeated from generation to generation.

Now the plant, with its special kind of roots, stem, leaves and flowers, is a very different-looking and much more complicated thing than either the male or female germ. The latter appear, even under the best power of the microscope, almost structureless. Yet in them there must be some principle capable of giving rise to the whole plant. That principle *must be* (but exactly how we do not know) contained in the substance or plasm of the germ-cell. And therefore the "germ-plasm" must have an ultimate constitution of extreme complexity. Also a constitution of a definite kind, because the germ does not give rise to any kind of plant but to a particular kind, having definite and recognisable characters of stem, leaves, flowers and so forth.

So we can see, dimly enough at first, that there must be something in the germ-plasm which we may call a "factor" (*i.e.* a thing which produces a result) for every individual character that the plant exhibits.

Exactly similar phenomena occur in animals.

Now we know well that the individual plant or animal—mankind himself—has an allotted term of life. The germ grows into the individual, the individual comes to maturity; when mature it reproduces new germs, and sooner or later after reproduction withers away and dies. The individual dies but the new germs carry on the race.

So the race does not die but is, potentially at least, immortal. The individual, however, is mortal. This was recognised clearly by Aristotle, and was a subject of deep reflection to Harvey, who wrote: "Facit namque hic circuitus gallinaceum genus sempiternum; dum modo pullus, modo ovum, continuata perpetuo serie; ex individuis caducis et pereuntibus immortalem speciem producunt" (Exercit. xxviii.). (This is the round that makes the race of the fowl eternal; now pullet, now egg, the series is continued in perpetuity; from frail and perishing individuals an immortal species is engendered.)

It was Sir Francis Galton, by his theory of "Stirps," and

Weismann by his much more fully worked out theory of the Continuity of the Germ Plasm, who gave us some real insight into this question.

The substance of the "egg"—*i.e.* the united male and female germ-cells—by growth and division expands into the individual, whose body is subject to all sorts of external influences from birth onwards and therefore exhibits individual variation within the limits illustrated by Johannsen's beans. But a portion of the whole, namely the germ-plasm, is set aside for reproduction. Sheltered within the individual's body, it is not exposed to the influence of the environment and remains unaltered (I will not say unalterable), and forms the material for the new generation. On this conception, which undoubtedly contains many elements of truth, the germ-plasm is continuous from generation to generation and practically *is* the race, with all its peculiarities and potentialities. The individuals, whose bodies are a by-product, as it were, of the germ-plasm, are the frail and perishing beings alluded to by Harvey. Their bodies are said to be composed of perishable *somatoplasm*, in contrast to the potentially imperishable *germ-plasm*.

It follows from this conception that the deviations from the mean, the changes, induced in individuals by the incidence of external agents, do not affect the germ-plasm, and therefore are not inherited.

The individual is relatively of no importance; the race is everything.

A critical analysis of all the available evidence has shown no authentic instance of the inheritance of changes of structure or habit which were acquired by an individual during his (or her) lifetime, and were distinctly "somatogenic," that is to say, affected only the somatoplasm of the individual in question.

In my opinion, as in that of most biologists, the proposition that somatogenic variations are not inheritable is as firmly established as any in natural science.

The moral and ethical deductions from this proposition are profoundly important, and must be taken fully into account

in any scheme for the betterment of the human race. For one thing it follows that many of the high hopes formed about improvement of the race through education are doomed to disappointment. Education cannot affect the germ-plasm; therefore its effects cannot be inherited. The process must be begun again in each generation.

Do not suppose, however, that the effects of education are negligible or of small account. The normal human individual is susceptible of improvement up to the limits of his inherited capacity. Through education, or the want of it, he may become a good or a bad citizen. If a good citizen, he can by precept and example hand on to his children what he has learnt, and they in turn will be better citizens and influence the generation that comes after. In this way a body of law, tradition and habit is acquired and handed on. It accumulates through spoken and written word, and has been in the past and may continue to be in the future the dominant factor in social improvement.

Education can do more than this. It can so impress upon individuals the universality and inevitableness of the natural laws and sequences to which they, in common with the rest of living nature, are subject, that they will strive to conform their inclinations to these laws, and to aim at a permanent and what I may call a germinal improvement of the race.

But this is a thing not to be hoped for if zoology is held in disdain, and the truths it teaches slighted or ignorantly denied.

I say "truths." It may be objected that all this story of the germ-plasm and the non-inheritance of acquired characters is nothing more than a theory; that theories have come into fashion, have been taken for truth, and then disproved again and again. You may say that I have, in this lecture, called into question the efficacy of Natural Selection, which every zoologist, a few years ago, would have declared to be a demonstrated law of Nature.

But I venture to say that we now stand on much more solid ground than we did those few years ago, and I will occupy the few minutes left to me in trying to show how much better

our evidence is than it was only fifteen to eighteen years ago.

I said just now that there must be in the germ-plasm a "factor" for every separate character exhibited by the individual body or soma. What do we know about these "factors"? Not all we may hope to know some day, but a great deal already, and there can be no doubt that they exist, and that in biparental reproduction they follow certain well-ascertained laws with the utmost exactness. By this I mean that the phenomena to which they give rise follow in uniform and invariable sequences.

The evidence rests upon what is generally known as "Mendelism," that is, the experimental study of breeding. It is also called "Genetics." Being strictly experimental, this evidence is of the highest scientific value.

We have to show that there are "factors" in the germ-plasm. I will take as an example of experiments demonstrating their presence the American fruit-fly, *Drosophila ampelophila*, recently the subject of much study by Professor T. H. Morgan and his collaborators. It is a small fly with red eyes, a greenish-grey thorax, the abdomen banded yellow and black, the single pair of wings grey, rounded at their extremities and projecting considerably beyond the abdomen.

In some individuals the wings are vestigial, reduced to little fin-like projections from the mesothorax. If a normal fly is crossed with a vestigial-winged fly, the offspring in F1 (the first filial generation) is normal, with long wings. When two of these offspring are interbred, their offspring (F2) appear in the proportion of three long-winged to one vestigial.

This is a definite numerical result and one cannot get numerical results unless there are units in question, which units behave independently. We may therefore assume the presence of units and construct the following scheme:—

Let ○ be a unit for "vestigial" and ● a unit for "long."

When the ♂ (male) and ♀ (female) cells of "vestigial" and "long" are united in fertilisation we get ○●. The individuals reared in F1 from this combination are all grey long, for ●, whenever present, always asserts itself, is

"dominant." These individuals, ♂ and ♀, form germ-cells, and in such a way that every germ-cell contains either ○ or ●.

Now when fertilisation between these germ-cells takes place, the following combinations are possible:

$$\underbrace{\begin{matrix} \bullet\,\male & \bullet\,\male & \circ\,\male \\ \bullet\,\female & \circ\,\female & \bullet\,\female \end{matrix}} \qquad \underbrace{\begin{matrix} \circ\,\male \\ \circ\,\female \end{matrix}}$$

and no others, as you can prove by experiment or by mathematics. The combination ○○ must have short wings, and these individuals, if interbred, only give vestigials. They are the so-called recessives. The individuals ●● have only the factor for long wings and they also breed true. But the individuals ●○ and ○● have both factors. They are long-winged because ●, when present, always asserts itself. But when interbred they always behave like the cross in F1, that is, they always produce offspring in the proportion 3 long: 1 vestigial.

The experiment is simply a repetition on an animal, the fruit-fly, of Mendel's original experiment with green and yellow peas. *Mutatis mutandis* the result arrived at is identical.

Hundreds of such experiments have been made with animals and plants, and always with the same result.

Though time forbids my going into details, in order to meet the objection that the scheme I have just given is only invented to account for the facts, I must tell you that germ-cells are not really simple things. In them, as in all cells, there are little bodies called *chromosomes*. When the germ-cells get ready for reproduction, or as we say "mature," these little bodies go through curious evolutions and divide and are distributed to male and female germ-cells in such a way that their products actually are sorted out in the manner shown in the scheme. These divisions and sortings out have been studied over and over again and are quite familiar to microscopists.

There is, therefore, a "mechanism of heredity," and we are dealing with facts, not with assumptions.

We can further show that, if more than one character is

tested, the factors on which these different characters depend act independently of one another.

Some individuals of *Drosophila* having long wings are ebony black. Flies with vestigial wings are grey.

If a cross is made between a grey-vestigial ♂ and an ebony-long ♀ there are two pairs of factors: "grey" with its alternative "ebony"; "long" with its alternative "vestigial."

In F1 all the offspring are grey-long.

But these, mated together, give in F2 offspring in the proportion 9 grey-long; 3 ebony-long; 3 grey-vestigial; 1 ebony-vestigial.

Time forbids my working out for you exactly how this happens, but I may say shortly that the result is precisely what is predicted by the mathematical computation of the combination of two pairs of alternative units acting independently.

And if three or four or more pairs of alternative units are brought into the account, it can similarly be shown that experimental results accord with mathematical calculation.

It is clear, then, that we are not indulging in mere speculation and hypothesis when we say that the germ-plasm contains factors which produce definite effects in the individuals developed from the germ, and that these effects follow mathematical laws. The examples given are simple. In many experiments much more complicated results are obtained, which often *seem* to stand in contradiction to the simple sequences just described. But careful analysis brings them all under the same law of unit characters in the germ-plasm. Often factors that appeared simple at first sight are found to be compound. And there are factors which by themselves produce no effect, but when brought into combination with other factors, or groups of factors, become active and produce startling results. Such factors are called "modifiers." And, most interesting of all, some factors seem to stick together and form "linkages," which are seldom, but occasionally, broken.

To all these statements two very legitimate criticisms may be offered:—

(1) What have all these experiments on fruit-flies and peas and other animals and plants got to do with man ?

(2) The characters enumerated and the factors that give rise to them are all small structural characters, and where is the evidence that mental endowments are subject to these laws ?

The answer to the first criticism is that a considerable number of characters in man have been shown to follow Mendelian laws. It is not possible, of course, to make exact breeding experiments with man, but by carefully collecting and recording the pedigrees of families affected by some peculiarity, it has been shown that colour-blindness, night-blindness, brachydactyly and a number of other characters are transmitted in accordance with these laws, some, such as colour-blindness, affording curious examples of sex-linked inheritance.

As to the second criticism, it is notorious that feeble-mindedness is inherited in man, and that is a mental character, if not exactly an endowment. There is another interesting fact which I have frequently witnessed and can personally vouch for the truth of. Many experiments have been made with mice. A common cross has been that between an albino mouse and a Japanese waltzing mouse. Both of these have red eyes, and in addition to other characters are peculiar for their *tameness*. They show no fear on being handled and do not try to escape.

When crossed together these two races give a hybrid in F1 which is very like but somewhat paler than the common grey ("agouti") house-mouse and has black eyes. When these hybrids are interbred a variety of forms are produced, among which there is always a certain proportion of grey mice indistinguishable from the common house-mouse. These greys are invariably *wild*, will not bear handling and are continually eating through and escaping from their cages. Tameness and wildness are mental characteristics. There is in this case a curious linkage between the external appearance and the mental habit, and it illustrates the statement of Morgan that a "factor" may control more than one character in the indi-

vidual. But in this case, and probably in many others, the grey colour depends on the co-operation of several factors, which, when all are present together, produce grey. But if any one or more is absent, other colours, or absence of colour, as in the albino, are the result.

The experiment just described is a good instance of the phenomenon of "reversion" to an ancestral character. The albino retained some and the waltzing mouse the remainder of the factors necessary to produce grey. When these are united a grey mouse results. Thus we have a simple explanation of a phenomenon that puzzled Darwin and many other students of inheritance.

Let us turn back for a moment to the fruit-fly, *Drosophila*. I said that in Morgan's flies a vestigial-winged form "appeared." So also did the form called "ebony." How did they "appear"? The facts are that out of a collection of many hundreds of ordinary flies some one, or perhaps two or three, individuals suddenly made their appearance with these peculiarities. Morgan tells us that in the course of five years' breeding of fruit-flies he found no less than one hundred and twenty-five new types, all of which bred true. Tower has given an analogous record for the potato-beetle *Leptinotarsa* (Doryphora). In both species some of the new types that appear in captivity are the same as types that may occasionally be found among wild flies or beetles. Indeed, Tower says that some of his new types were identical with local races of potato-beetles established in the Southern United States or in Mexico. There are several cases in which it has been shown that new types appearing in confinement are paralleled by types existing in nature, and this is important, for it shows that the changes are not due to artificial conditions.

Such new types are said to arise by "mutation" and are called "mutants." They are often strikingly different from their parents, and they appear suddenly with their full characters. There is no question of a series of gradations, accumulating through several generations, till the new type is reached. As they hand on their peculiarities to their descendants in conformity with Mendel's Law of Segregation, they must owe

their origin to a germinal modification. But how can we explain their abrupt arrival on the scene ?

It has been proved that, in a great many cases, the exhibition of a " mutant " is due to the combination of factors previously segregated in different individuals of a population. We have seen that there are " modifying " factors, which only produce an effect when brought into combination with two, three, or even more factors which, in the absence of the modifier, give quite a different effect. Experiments, supported by mathematical calculation, have shown that a single factor may be so isolated in the course of breeding that it survives only in a very small percentage of the individuals composing a general population. And many mutants owe their origin to the mating of an individual possessing such a modifier in its germ-plasm with another individual having the appropriate factors on which the modifier can work.

The reproduction of a grey mouse from the cross albino and waltzing mouse illustrates this point, as well as giving an explanation of the puzzling problem of reversion. It further illustrates the fact that factors do get separated in different individuals, for both albino and waltzing mice were undoubtedly originally derived from ordinary grey mice, and the one race has lost factors which the other has retained, and *vice versa.*

Professor Morgan is inclined to the opinion that all mutations are due to the recombination of such isolated factors, and that the improvement of a race by selection is a process of picking up a series of modifiers by selective breeding.

But this view presents great difficulties. It involves the belief that every species was, at some time, endowed with a stock of factors, which can be sorted out and recombined again by the mechanism of heredity, but are themselves unchangeable. If this were so, it would be impossible to account for all the variety of the animal and vegetable world.

The alternative view is that factors are changeable; and the most probable view is that they are changed in consequence of some physical or chemical alteration in their environment, which is the " soma " or body of the individual in which they are carried.

There is nothing inherently improbable in the theory that the factors of the germ-plasm may be affected by chemical and physical changes in the soma. Nor does it stand in contradiction to the established principle that it is only germinal and not somatic changes that are inherited. For we are now postulating a germinal change, and that is all that is required.

Tower claims that he has produced germinal changes in the potato-beetle, mainly by the combined action of heat and moisture, such changes being evidenced by the excessive production of mutants in the next generation. And there is other evidence pointing in the same direction.

But, after passing it in review, it must be confessed that the available evidence on this point is insufficient, and we are still ignorant of the causes which may produce changes in factors, and still more ignorant of how new factors come into existence.

All that we do know is that many of the factors that operate in plants are chemical, and there is good reason for believing that all the so-called "factors" are chemical bodies, often of great complexity. Such highly complex molecules may, under conditions not accurately known to us, take up a fresh molecule of some element, and in so doing entirely change their character.

But such a hypothesis, though not improbable, is highly speculative in the present state of our knowledge. I do not propose to pursue the subject any further, beyond stating my belief that factors are susceptible of change, by some means not yet ascertained.

Now that I have passed from the region of ascertained fact to the borderland of speculation, I will conclude by indicating, as briefly as possible, what definite lessons are to be learnt from the biological researches of the past fifteen years.

You will agree, I hope, that experimental zoology and botany have picked up a number of new factors which so modify earlier doctrines that we must reconsider the moral and ethical standards founded on those doctrines.

It has been my purpose—though I am afraid that I may seem to have wandered a good deal from it—to urge that a sound knowledge of zoological science is an indispensable

element in education, because without it we cannot appreciate the importance and the reality of a number of fundamental problems bound up with the very nature of man.

As regards the doctrine of Evolution in the animal kingdom, and its application to human affairs, I have argued that it is the basis of all our hope of progress and betterment in this world. For if we deny evolution, we deny the possibility of change, and progress is change for the better.

But a pious belief in evolution is not a sufficient guide to our conduct. If we would act rightly we must understand clearly how evolution has come about, to what laws it is subject, and whether those laws can be modified or set aside by man to his own advantage.

I have been at some pains to convince you that the current doctrine, that evolution in animals and plants depends upon a ratio of increase so high as to lead to unrestricted competition among the individuals of a species, and in consequence to a Struggle for Existence, with extinction of the less fit and Survival of the Fittest, no longer commands the universal assent of zoologists. Indeed, it has been seriously undermined by the discoveries of recent years.

It is at the best a melancholy doctrine, and if it is not in itself immoral, some of the deductions drawn from it certainly are immoral.

We must ruefully admit, for past history and present circumstances force the admission, that man does compete bitterly and to the death with his own kind. But this fratricidal war is not so evident—I doubt whether it exists to any great extent—in the animal world.

It is to be attributed to a want of adaptation in man after he had, by the exercise of his reasoning faculties, obtained such dominion over the brute creation that he became practically immune from the attacks of predaceous animals, and is becoming increasingly immune to the attacks of disease-producing micro-organisms. Because of his pre-eminence, he multiplies without any serious check and has become an enemy to himself. Though he has succeeded in obtaining the control of the rest of creation, he has not yet succeeded

in obtaining control over himself. Hence the grave disharmony that we see in social and international affairs, and are experiencing so acutely at this moment.

Both the authors of the doctrine of Natural Selection and their followers have realised fully this aspect of their teaching, and have sought to justify the evident evil said to be inherent in Nature by such considerations as those given in the sentence quoted from Darwin. Wallace deals with the question in much the same way and at much greater length.

None the less there remains the appalling verdict that it is through war, famine and death that the highest organisms are evolved. It is evident that this justification fails in its application to man. If it be the case, as it undoubtedly is in large (but not in whole) measure owing to their preying upon one another, that animals have been evolved through the operation of internecine warfare, we may, from an ethical point of view, regard the fact with equanimity. Our moral sense is not shocked by the statement that in the brute creation a very high ratio of increase is a favourable adaptation, enabling a species to maintain its average numbers in the presence of a host of enemies. There is a vast sacrifice of individuals for the benefit of the race, but the sacrifice falls chiefly on the young and scarcely sentient forms, and even the adult individuals have not the apprehension of death, the acute sense of pain, or the feelings of compassion and sympathy which in ourselves render the holocaust so shocking.

We do not imagine that there are philosophers among fishes or rabbits to lament over the misfortunes of their kind. Therefore we find no cause for offence in the zoological doctrine that the race is all-important, the individual matters nothing.

But with mankind the case is very different. The faculty of reason by which he transcends the beasts is an *individual* faculty. It is the self-conscious Ego that hopes and fears, that mourns or is glad, is contented or discontented, happy or miserable. The well-being or misery of a nation is not collective, but the sum of the individual happiness or misery of the individuals composing it.

Therefore we cannot view with equanimity, still less with moral approbation, conditions involving a vast production with a concomitant vast waste of human life and all the misery attendant on the waste.

It is certain, and no sophistry can remove the certainty, that a great increase in the numbers of a population will lead to competition ; and the larger the numbers, the keener and more cruel will be the competition.

The labouring classes, upon whom the stress of competition chiefly falls, are impelled by a sound instinct when they cry out against our present social order, and demand that competition should be restricted if not entirely abolished. They have various and not altogether consistent schemes for attaining the desired end, but have they considered the fundamental facts taught by zoological science, and the inexorable laws to which mankind, in common with all animal nature, is subject ?

Perhaps not, but they may urge with some justice that hitherto zoological "laws," as they are called, have been interpreted to the disadvantage of themselves and to the advantage of the so-called "privileged classes."

It has been confidently asserted that it is a fundamental biological law that progress is only possible through competition, and that with cessation of competition, degeneration of the race must follow.

But is this a true inference from the facts ? I may remind you of the quotation from the most recent work of one of the most distinguished authorities on breeding and inheritance, Professor T. H. Morgan : "New and advantageous characters survive by incorporating themselves into the race, improving it, and opening to it new opportunities. In other words, the emphasis may be placed less on the competition between the individuals of a species . . . than on the appearance of new characters and modifications of the old characters that become incorporated in the species, for on these depends the evolution of the race."

Competition is not necessary for improvement. That removes a great load of difficulty in schemes for social reform.

But observe, the conclusion gives no sanction to such visionary ideals as natural equality of individuals. "New characters" and "modifications of old characters" are the things on which progress depends, and their very existence implies inequality.

Competition may be eliminated, without fear of harm, but if we are to construct anything permanent, anything better than a temporary shifting of the balance of misery and waste, it is necessary to look ascertained facts and well-founded scientific conclusions squarely in the face, and to found our plans on them, rather than on visions of what might be if the course of Nature were different from what it is.

The fundamental facts are reproduction and inheritance. So long as we did not know their laws they could not be controlled wisely. Now we do know their laws, and they can be controlled. It is time that man set about to obtain the same mastery over himself that he has long ago obtained over the beasts of the field.

The first step is the control of the birth-rate, without which restriction of competition is impossible. The bare suggestion raises a howl from a large number of persons, but the loudest howls come from those who are framing schemes for greater competition, for commercial aggrandisement in the reconstruction after the war. "Non ragioniam di lor, ma guarda e passa."

Others say it is immoral, or that it is impossible.

"Immoral" it cannot be, if right methods are followed and the aim is so beneficent. "Impossible" I do not accept; but difficult it certainly will be, and its operation exceedingly slow.

For any change in our social habits and customs in this respect must be the outcome of individual reason and intelligence working towards a moral end. That is to say, it must be the result of education of the people; an education sufficiently sound to bring conviction to all. Then, and not till then, will man by the exercise of his reason get dominion over himself and escape from his present troubles, even as his primitive forefathers got dominion over the beasts and escaped from them.

It is not a question for State regulation, and in my opinion

the ill-considered suggestions of eugenic enthusiasts have done the cause much harm. A food controller would be in an enviable position as regards popularity in comparison with a marriage controller.

This is eminently a question in which the self-conscious Ego, the individual, asserts himself, and one in which the doctrine of sacrifice for the good of the race is not applicable, unless it be a voluntary sacrifice of appetite and incontinence. And though I do not intend to press this matter further, I may remind you that every great religion has laid stress on such voluntary sacrifice in this very matter.

The same education that taught continence would teach the importance of inheritance in the improvement of the race, and would make men and women more seriously alive to their responsibilities.

Nowadays, when a marriage is in contemplation, it is the dowry of money or lands or household effects that is considered—useful and indispensable things no doubt, but exceedingly evanescent. What of the far more important and unalterable dowry of inherited and inheritable characters that every man and woman possesses? What thought is given to these?

No doubt there has been much foolishness attached to family pedigrees, and among many who think themselves very intelligent everything that has to do with descent and ancestry is looked down upon with contempt and derision. I offer no defence for arrogant pretensions founded upon supposed or even proved descent from Norman blood, but these very intelligent persons are wrong, and quite as arrogant in their way as those whom they affect to despise.

They might learn much and greatly modify their views by a study of pedigrees as constructed by the late Sir Francis Galton, by Professor Karl Pearson, and by students of Mendelian inheritance.

It is, perhaps, an unattainable ideal, but I would wish to see every man and every woman interested in the family pedigree, of which a record should be kept in every household. It should be a source of pride to be able to point out several

generations of honest, serviceable members of the community, none of whom had ever brought discredit on the family name. It should be a matter of solicitude that no taint, in other words unfavourable factors, should be introduced by marriage, and public and family opinion should discourage the transmission of such taints, physical or mental, as the records might show to exist. Nothing but good, and great good, could result from such an awakening of interest and responsibility.

There are, I know well, many humble homes which maintain a proper family pride, and could, if records had been kept, point to an ancestry which for consistent well-doing would not suffer in comparison with more pretentious pedigrees. And from such families individuals arise, and have arisen throughout history, who have attained positions in which they have done good and even great service to the State. But many more fail to realise their potentialities for lack of opportunity. An improved social system should redress this inequality. Mutations, whether in the shape of the production of new factors, or in the shape of the combination of factors distributed among individuals of the population, are always proportionate to numbers, and therefore most frequent in the most numerous class. In all classes there will be unfavourable as well as favourable mutations, but in a "good stock" the chances of desirable mutations will be the greater, because in such a stock there will already be an accumulation of favourable factors.

I will conclude by calling your attention to a statement of Weismann's, cordially endorsed by Darwin and supported by the most recent investigations: that in every case of modification there are two factors (the term is not used in its technical sense), the nature of the environment and the nature of the organism, and the latter is much the more important of the two. Hitherto all sociological effort has been directed to the environment. Is it not time to accept the teaching of zoology, and to pay some attention to the nature of the organism, which is so much more important, and, I may add, so much more certain in the effects it produces?

III

MUSEUMS AND RESEARCH

By C. TATE REGAN, M.A., F.R.S.
Of the British Museum (Natural History).

III

MUSEUMS AND RESEARCH

Museums are of many kinds and they serve many purposes; but all have one common object, the preservation of material for education and research.

When Professor Dendy invited me to give this lecture—one of a series designed to emphasise the national importance of Zoology—he suggested that I might take as my subject the educational value of museums; but it seemed to me that at the present day the educational value of museums is appreciated to a much greater extent than the fact that museums are—or ought to be—centres of research, and that in a museum of Natural History research may be more important than education.

Certainly one of the purposes of a zoological museum is to arrange, display and label series of animals in such a way as to interest visitors and give them a general idea of the animal world; moreover, these exhibits should be sufficiently complete to be of value to zoological students and to other visitors in search of information, whilst special exhibitions may illustrate the relation of zoology to the intellectual life and material welfare of the nation. But another of the principal objects of a zoological museum should be to amass collections of animals, not for exhibition to the public, but for scientific study. In an ideal museum every species would be represented by a series of examples illustrating its geographical range, variation, growth, seasonal changes, sexual characters etc., and all these specimens would be properly preserved, correctly named, labelled, catalogued and arranged in systematic order according to their natural relationships.

No such museum exists or ever will exist; but the Natural History Museum at South Kensington probably comes nearer to this ideal than any other in the world. To give some idea of the size of the collections, and at the same time of their incompleteness, I may say that the collection of Fishes, for which I am responsible, numbers more than 100,000 specimens, representing perhaps about 13,000 out of some 20,000 known species. The collection of Fishes is preserved in spirit and is bulky, but is small in numbers compared with some of the other collections. The Birds, the most complete collection in the world, number some 500,000 skins and 100,000 eggs, whilst the Insects total about 3,000,000 specimens.

The Natural History Museum is not a zoological museum only; nevertheless 31 out of a total of 43 members of the permanent scientific staff are zoologists, belonging to the departments of Zoology, Entomology and Geology, and I need hardly say that many times that number of zoologists, who come from all parts of the world, find plenty of material to work on in our vast national collections.

Zoological research in our universities may be morphological or physiological, but one very large and essential branch of zoological research, systematic work, the classification of animals, can only be done properly with the aid of large collections, such as those preserved in our National Museum and in other great museums of the world. These collections are permanent, they are records of past work to which students of the present must refer, and as such they are the basis of all systematic work, and to a large extent they are the basis of other zoological work as well.

The systematic zoologists who form the scientific staff of a zoological museum are, of course, specialists, each devoting himself to some particular group of animals. The specialist in a museum need never be idle; in addition to curatorial and routine work he may, if he can find the time, monograph some order, family or genus, and rearrange part of his collection accordingly. New material is continually arriving, and the new specimens have to be named and put away in their proper place; often reports, including descriptions of forms new to

science, have to be written about them for publication. This work is endless, for each hitherto undescribed species to some extent modifies our conception of the relationships of those already known and may demand a reclassification of the genus to which it belongs.

Now the question that will at once occur to you is this: What is the good of this museum work? Are the systematic zoologists and their systematically arranged collections of any use? I will try to answer this by showing, firstly, the relation of systematic zoology to zoology generally; secondly, the utilitarian value of systematic zoology, and thirdly, its importance for philosophical zoology.

First, then, as to the relation of systematic zoology to zoology generally. The systematic zoologist seems to me to stand midway between the anatomist, who studies the structure of some particular type or of some organ or group of organs, and the biometrician, who makes a statistical study of the variation of a species on large numbers of individuals.

The systematist is himself an anatomist of a sort, but he takes a wide and rapid survey of the structure of a group of animals in order to seize on those characters that indicate relationship and can be used in classification. Similarly the systematic zoologist is, in a way, a biometrician; but he studies variation in a much larger number of species, and as a rule on a much smaller number of individuals of any one species, than the biometrician proper. The systematist thus obtains results that may be important and suggestive for the anatomist on the one hand and the biometrician on the other, just as their work is valuable for him.

Anatomy, systematic zoology and biometry are branches of animal morphology, they grade into each other, the distinction between them is arbitrary and the connection between them is direct and intimate. The relation of systematic zoology to physiology is less direct; but all zoologists are dependent on the systematists and their systematically arranged collections in one respect, that is, they must go to them to get animals correctly named. The correct name of an animal is a clue to all that is known or that has been

recorded in literature about its structure, habits, economic importance or anything else; without the correct name we are in the dark and the conclusions we arrive at may be founded on erroneous grounds. It is most important that the anatomist or the physiologist should know exactly what species he is dealing with. In many cases conflicting statements that have been made about the structure of an animal, or contradictory observations about its behaviour, have been found to be due to the fact that the species had been wrongly identified.

An historical case, discussed by Darwin in his *Animals and Plants under Domestication*, is that of the rabbits introduced from Spain into the island of Porto Santo, near Madeira, just 500 years ago. These ran wild and increased at such a rate that they became a pest; in 1861 two were brought alive to this country and Darwin observed that they were smaller than and differently coloured from the English wild rabbit; he concluded that a distinct species had evolved on the island of Porto Santo. But this conclusion was wrong, for Mr. Miller, in his *Catalogue of the Mammals of Western Europe*, tells us that these Porto Santo rabbits are exactly like those of Southern Europe, whence their ancestors came, whilst a larger and somewhat differently coloured race inhabits Central Europe and the British Isles. Contrary to what Darwin believed, the Porto Santo rabbit has not changed at all since its introduction 500 years ago.

A similar explanation applies to claims made in recent years that new species of fishes have evolved in a comparatively short time, one in a canal in France, another in a lake in Germany; in each case the wrong species has been selected as the supposed ancestor.

The relation of systematic zoology to general zoological research may be summarised as follows: the classification of animals is in itself an important and essential part of zoology, and it is of value to all other branches of zoology because by its means animals can be correctly named. I pass then to the second question, the practical value of systematic zoology.

Economic zoology is sometimes spoken of as a thing apart,

but in reality it is most intimately related to and is dependent on systematic zoology, for all economic work is based on a knowledge of species and of their distribution. It is true that the Imperial Bureau of Economic Entomology is quite distinct from the Entomological Department of the Natural History Museum, but it has made the Museum its headquarters in order to use the collections that have been arranged by the entomologists who are not specifically labelled "economic," and here the entomologists of both departments co-operate in the campaign against the insect enemies of man, especially the carriers of disease and the destroyers of food.

Insect pests are so numerous and may do such incalculable damage if they are not held in check that the economic importance of other groups of animals is rather overshadowed by them. Nevertheless all animals have some relation to human affairs and it may be of interest to enumerate some of the ways in which the group that I have specially studied, the Fishes, are of importance to man. In the first place, of course, a great many kinds are used as food; fishes also yield a number of valuable products such as oil, glue, isinglass, fertilisers etc.; some species are important principally because they are eaten by food-fishes. A good deal of attention has been given of late to fishes that eat mosquito larvae and so help to check malarial fever. Again, as fishes can swim, see and hear under water the naval engineer may perhaps learn something from their form and structure, and their coloration also is worth study, for many fishes are camouflage experts.

In all these ways fishes may be useful, but there are many harmful species: quite a number have poisonous flesh; some will attack man directly if they find him in the water, either to eat him or to inflict poisonous wounds; others prey on food-fishes or other animals of economic value; fishes even cause trouble by damaging submarine cables, and on several occasions we have received at the Natural History Museum parts of cables that had been bitten into by fishes which had left a tooth behind; sometimes the tooth has enabled us to identify the species.

We get many other fishes or parts of fishes sent for identification: for example, frozen fish from Canada and South Africa; tinned fish from Portugal, California and India; strips of shark-skins of unknown origin; fishes that eat mosquito larvae, sent by medical officers from East Africa, Mesopotamia and Salonica; all these can be named by comparison with specimens in the collection at South Kensington, and there is no other institution in the Empire where this can be done.

Systematic study of the species of fishes and of their distribution and habits is the foundation of fishery development and fishery legislation, and the economic importance of fishes has led me to insist on the fact that all work connected with the conservation and arrangement of the collection of fishes in the Natural History Museum is economic work.

I have mentioned insects because their economic importance is so well recognised, and fishes because that is the group that I know most about, but all groups of animals are more or less directly useful or harmful to man, and must be systematically studied. The great value of systematic work on extinct animals is not generally recognised, but geology depends on the accurate determination of fossils. They are the clue to the age, sequence and nature of the rocks that contain them; from them we learn in what localities and at what depth we shall find coal and other minerals, or where to look for oil or for water.

I have treated this part of the subject very shortly, and I may refer you to an article entitled "National Work at the Natural History Museum" in the *Museums Journal* for February 1918 for a more detailed exposition of the practical utility of the Museum, with examples of the matters that are referred to that institution for information and advice.

So much, then, for the utilitarian value of systematic zoology: I now pass on to its relation to philosophical zoology.

Evolution is no longer a hypothesis—it may be termed an established fact; but the causes of organic evolution are matters about which we may theorise to any extent. Of recent years the experimental zoologists, the practical students

of heredity, have tried to solve the great problem of the origin of species by new methods and with results that they regard as satisfactory. No one can be more sensible than I am of the great theoretical interest and practical utility of the results obtained by the experimental study of the science of breeding; but—speaking as a systematist—I must confess that these results seem to me to throw but little light on the origin of species and still less on the evolution of adaptations.

With regard to the propriety of a systematist speaking on this subject I cannot do better than quote some sentences from Professor Dendy's presidential address to the Quekett Microscopical Club in 1916:—

"Some of us think that the science of biology includes the study of the whole organic world in all its aspects, and that the systematic description and arrangement of plants and animals constitutes an indispensable part of the foundation upon which all biological theory must be based. Indeed, I would go further, and even say that no biologist without some considerable experience of systematic zoology or botany is really competent to form a judgment on such problems as the nature and origin of species and varieties. The true systematist is just as much inspired with the enthusiasm of research and the thirst for knowledge as the experimental biologist. The difference between the two lies in the fact that the experimental biologist confines his attention to the solution of certain fixed and definite problems suggested by his own very limited knowledge of the organic world, whilst the systematist studies the results of the infinitely varied experiments which Nature has been performing upon living organisms ever since they first appeared upon our planet."

The systematist indeed often gets very clear indications as to where, when and under what conditions species may have originated; I will illustrate this by some examples from my own work.

Many marine fishes are anadromous—that is to say, they ascend rivers to breed in fresh water. Such fishes often form permanent fresh-water colonies, in rivers or in lakes, and in course of time these may become distinct races or even species.

The Twaite Shad (*Alosa finta*) of the Atlantic coasts of Europe and its Mediterranean representative (*A. nilotica*) are fishes of the Herring family that run up the rivers to breed. In the large lakes of northern Italy there are Shad that never go to the sea, and are quite distinct from the migratory form that enters the lakes at the breeding season. It is not generally known that a Shad inhabits the Lakes of Killarney; it is closely related to the Twaite Shad but has a deeper body and more numerous gill-rakers, characters that may be adaptive, for the form of the fish is related to its way of swimming and the number of the gill-rakers to its food. We may regard the migratory Shad as the parent species and the lacustrine forms as their children, and it seems clear that the initial step in the formation of these local races was a change of habits; some of the Shad that entered the lakes to breed stayed there to feed.

Another case of some interest is that of the Char (*Salvelinus*), fishes of the Salmon family. Char are essentially fishes of the Arctic Ocean, running up the rivers to spawn and often forming lacustrine colonies of fish that do not visit the sea; in the sea they do not come nearer to the British Isles than the coasts of Iceland and northern Norway, but non-migratory races of Char are found in the lakes of Scandinavia and of the Alps, and in our islands in Ireland, Scotland, the Lake District and North Wales. Similarly Sea-trout are found from Iceland and Norway to the Bay of Biscay, but non-migratory Trout so far south as the rivers of Algeria and Morocco.

It is evident that during the Glacial Epoch Char occurred on our coasts and ran up our rivers, and Sea-trout ranged southward to northern Africa, and that when the climate became warmer, and the southern limit of the marine range of these anadromous species shifted northward, Trout remained in the rivers of the Atlas Mountains and of southern Europe, and Char in many lakes of the British Isles and of the continent, as relict forms. The Char of different lakes are distinguished from each other especially by form, coloration, scaling, size of the fins, size of the eye and structure of the

mouth: characters that may be regarded, for the most part, as connected with differences of environment and of habits. Sometimes the Char of neighbouring lakes are quite dissimilar.

In the case of the Char physical isolation has followed habitudinal segregation, and I think every systematic zoologist recognises that physical isolation has often been a condition of the evolution of species. A community may become split into two or more by physical barriers that prevent intercommunication, or part may become separated from the parent stock by migration into a new area; under these circumstances geographical or representative species may arise, one form inhabiting one area, its nearest relative representing it in another —usually an adjacent—area.

One cannot get a better idea of the effects of physical isolation than by comparing the marine fishes of the Atlantic coast of Central America with those of the Pacific coast. The fishes of the two coasts are very similar, and a number of the Atlantic species are represented on the Pacific side by forms that can only be distinguished from them by a detailed comparison. In other words, taking the fishes of the Atlantic and Pacific coasts together, a large proportion can be grouped into pairs of closely related species, one member of each pair on the Atlantic coast of Central America and the other on the Pacific coast.

There is good reason for believing that in Eocene times there was a marine connection between the Atlantic and Pacific oceans across what is now the Isthmus of Panama, and that in the Miocene this connection came to an end, and there can be little doubt that each pair of species is descended from a parent species that was found on both coasts when the two oceans were connected.

I have given examples to show that habitudinal segregation, habitudinal segregation followed by physical isolation, or physical isolation alone, may have been the conditions under which new subspecies or species have arisen.

It often happens that two or more species inhabit the same area under circumstances that indicate their derivation in that area from a single ancestral type; in such cases, whenever

they have been properly investigated, it has been found that these species differ in habits. Sometimes such species may differ markedly in adaptive characters but show close agreement in all other features.

Two species of fishes of the Herring family—of a type peculiar to Lake Tanganyika—are so similar in appearance and in nearly all other characters, even in details of coloration, as to leave no doubt as to their very close relationship ; indeed, they were originally described as one species, *Pellonula miodon* ; nevertheless I have shown that these two forms differ in a most remarkable manner in the structure of the mouth and in their dentition.

The Cichlidae are a family of Perch-like fresh-water fishes in which the lower pharyngeals, a pair of bones in the throat that bear teeth, are joined together. Two species of this family from Western Ecuador are so like each other that they were originally described as one, *Heros festae*. But in one, as in several related species found elsewhere, the lower jaw projects, the teeth in the jaws are sharp, the pharyngeal teeth are conical and the pharyngeal bones are merely coalescent by their straight inner edges to form a triangular plate of moderate size ; in the second species the lower jaw is shorter than the upper, the jaw teeth are blunt, the pharyngeal teeth form a flat pavement and the bones that bear them are united by a deeply interlocking suture to form a broad and massive plate. It is clear that the first species is predaceous, and I have proved that the second feeds on molluscs by finding the stomach full of broken shells. I believe that a part of the ancestral stock gave up chasing little fishes and took to eating shell-fish on the bottom, and that this was the initial step in the differentiation of the two species.

I will now pass on to some more striking instances of adaptive evolution. The Cyprinidae—the Carp family—are fresh-water fishes of Europe, Asia, Africa and North America ; the mouth is toothless, but the pharyngeal bones, in the throat, bear teeth that bite upwards against a horny pad supported by the base of the skull, and these teeth vary in form, number and arrangement, according to the nature of the food.

Now in mountain streams of the Malay Peninsula and Archipelago there is a curious Cyprinid genus—*Gyrinochilus*—which agrees with another genus from the same region—*Crossochilus*—in most characters: form, fins, scaling etc. But *Gyrinochilus* differs from *Crossochilus* and from all other fishes of the Carp family in several features connected with its peculiar habits; it has taken to feeding on mud and has lost its teeth, whilst the bones in the throat that usually bear teeth are almost vestigial, and the horny pad they bite against in other fishes of the Carp tribe has disappeared. Moreover, as mud is not very nutritious, the fish has to extract the nourishment from a large quantity at a time, and for this purpose the intestine is very long—fourteen times as long as the fish itself. Another peculiarity is that the lips surround the mouth and form a funnel-shaped sucker by means of which the fish can hold on to stones in the torrents, and this is no doubt useful also in gathering in the mud; anyhow, whether the fish is holding on to stones or has its mouth full of mud, it cannot take in water for respiration through the mouth in the usual manner; this difficulty is overcome by having the external opening of the gill-chamber divided in such a way that the water flows in through the upper part and out through the lower.

Now if—as some experimental zoologists would have us believe—evolution has proceeded by the sudden appearance of new mutations and definitely inherited variations, some of which will find an environment to which they are more or less well fitted—if, in short, change of structure has preceded change of function—we must regard *Gyrinochilus* as singularly fortunate in that, although it has lost its teeth, it has managed to do without them because it has acquired an intestine sufficiently long to enable it to live on mud; and its good fortune has not ended there, for it has been able to use the sucker which has been formed by the union and outgrowth of its lips because, by a marvellous coincidence, it has evolved an apparatus which permits it to breathe without taking in water through the mouth.

Gyrinochilus has not changed its form or its fins, but has

become modified in relation to new methods of breathing and feeding; it is of some interest to compare with it a fish that has retained its apparatus for breathing and feeding unmodified, but has completely changed its form.

The Blennies are little shore-fishes, very characteristic of rock-pools. One Indo-Pacific genus—*Petroscirtes*—is a typical Blenny in most respects, and is characterised chiefly by having the gill-opening reduced to a small hole and by the presence

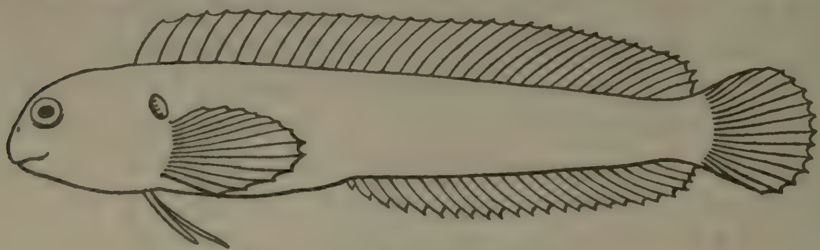

FIG. 1.—*Petroscirtes elegans.*

FIG. 2.—*Xiphasia setifer.*

of a pair of canine teeth in each jaw, the lower pair being very strong and curved, in comparison with the size of the fish almost as large as the canines of the Sabre-toothed Tiger.

Now *Petroscirtes*, like other Blennies, is moderately elongate, has about 30 to 40 vertebrae, about half of which belong to the tail, and has a well-developed tail-fin and broad-based pectoral fins. There is another Indo-Pacific genus, *Xiphasia*, evidently very closely related to *Petroscirtes*, for it has the same curious dentition and the same small gill-openings. But *Xiphasia* is very elongate in form—eel-shaped; the

vertebrae have increased in number from 30 or 40 to about 125, of which about 110 belong to the tail; the tail tapers and ends in quite a small fin, and the pectoral fins are narrow, just as they are in eels. We can only interpret *Xiphasia* as a *Petroscirtes* that swims, not like a blenny, but like an eel, that is, by undulating movements of the long tail and long median fins, and we can only believe that it has evolved from a *Petroscirtes* in adaptation to new habits that necessitate a new method of swimming.

All the facts, as I see them, lead to the conclusion that evolution has been mainly adaptive and that a change of structure has followed and has not preceded a change of habits. Can one really believe that the Flat-fishes originated from fishes that found themselves with both eyes on one side of the head and decided to make the best of it by lying on one side with the eyes uppermost?

I am far from claiming that all systematists would agree with the views I have put forward. All I wish to insist on is that systematic zoology does form a groundwork for the study of such problems as the origin of species and the evolution of adaptations, and makes no mean contribution to the elucidation of other problems, such as the past history of oceans and of continents.

I have tried to give you some idea of the nature, scope and value of the work that may be done in a zoological museum, such as the Natural History Museum at South Kensington. I have attempted to show you that this work, the classification of animals, is an essential part of pure zoology, is the basis of economic zoology, and is, to a large extent, the foundation of philosophical zoology. The collections remain as a permanent record of the work done, and are available for reference and for study. It is, I believe, necessary for the intellectual development and the material prosperity of the nation that this work should be carried on.

But are these things generally understood in this country?

I have often tried to find out what sort of conception of the museum and its work people have. The old idea that a

museum is a sort of Barnum's Show—a place for the exhibition of freaks—is not entirely dead.

Not long ago two little boys came up to me in the Central Hall of the Natural History Museum and asked the way to the "curios of nature." I said, "What do you mean by that?" and one replied, "The two-headed cats and such-like things." I asked why they wanted to see them, and the answer was, "Well, sir, they make us laugh."

I think the majority of our visitors place us on a higher level than that, but it is astonishing how few of them have any idea of the work done behind the scenes. Many of them think that the museum begins and ends with the exhibition galleries and that the staff consists of commissionaires and policemen; and if that is the case with the people who visit the museum, it is even more so with those who never come near it.

With our present system of education it is perhaps not surprising that the public should fail to appreciate the relation of a zoological museum to the development of the resources of the Empire. But I must confess that it was something of a shock to me to read the recently issued reports of the Advisory Council to the Committee of the Privy Council for Scientific and Industrial Research; this Advisory Council included seven scientific men of great eminence—chemists, physicists and engineers—but no biologist.

When this Committee was appointed it was arranged that the Advisory Council should "keep in close touch with all Government Departments concerned with or interested in scientific research," by inviting the departments to appoint officers to act as assessors, to advise and assist the Council and attend its meetings. The assessors represent the following departments: Admiralty, Board of Agriculture and Fisheries, Air Board, Development Commission, Colonial Office, Board of Education, Home Office, India Office, Irish Office, Local Government Board, Medical Research Committee, Ministry of Munitions, Scottish Education Department and the Board of Trade; but there is no assessor from the Natural History Museum, which was evidently not regarded as a Govern-

ment Department concerned with or interested in scientific research.

In their report the Council deal with the national institutions engaged in scientific research, particularly the National Physical Laboratory, the Imperial Institute and the Imperial College of Science, and they endeavour to complete the list in a footnote which runs as follows: "The work initiated under the Development and Road Improvement Funds Acts of 1909 and 1910, the work of the Medical Research Committee and that of the Home Office Testing Station at Eskmeals are omitted from this review, which deals only with the development of industrial research." Here again the Natural History Museum is not mentioned at all; it is not found worthy to figure on a list of national institutions engaged in scientific research.

I am precluded by my official position from saying anything about the recent attacks on the Museum by other Government Departments, but I may remind you that Professor Dendy, in the opening lecture of this series, noticed this example of incapacity to understand the importance of the Natural History Museum, and that Professor Bourne in his lecture referred to the treatment of the Natural History Museum as showing how little zoology is valued in this country.

But, at any rate, things are not so bad nowadays as they used to be. In the days before the Natural History collections of the British Museum were moved to South Kensington, the Zoological Department was housed in an underground dungeon, in the gloom of which many of the catalogues of the collections were written. The department was thus described in 1877 in a review in *Nature*: "If the visitor to the British Museum will pause at the foot of the staircase leading up to the palaeontological gallery and look carefully into the obscurity in the right-hand corner he will perceive a door with a brass plate on one side of it. On entering this door and descending (with care) a flight of darkened steps, he will find himself in the cellar, which has for many years constituted the workshop of our national zoologists. Two small studies partitioned off to the left are assigned to the keeper of the department and

his first assistant. The remaining naturalists are herded together in one apartment commonly called the ' Insect-room ' along with artists, messengers, and servants. Into this room is shewn everybody who has business in the Zoological Department of the British Museum, whether he comes as a student to examine the collections or as a tradesman to settle an account. —No lights are allowed, and when the fogs of winter set in the obscurity is such that it is difficult to see any object requiring minute examination. Under these circumstances, it is more than creditable to our zoologists that they should have turned out the large amount of scientific work that has issued from their department of the British Museum during the past thirty years."

That gives some idea of the status of a zoologist forty years ago, and makes one feel that if, at the present day, zoology does not occupy the place that it should, at any rate we are better off than we were in the past, and we may have some hope of the future.

IV

MAN AND THE WEB OF LIFE

By J. ARTHUR THOMSON, M.A., LL.D.
Professor of Zoology in the University of Aberdeen.

IV

MAN AND THE WEB OF LIFE

The two strongest tendencies of our age are probably the democratic and the scientific. The keywords of the democratic tendency are such as participation in responsibilities and rewards, liberation, equality of opportunity, solidarity. The keywords of the scientific tendency are such as accuracy, verification, prevision, control. Now, as a condition of secure progress, it seems greatly to be desired that these two strong tendencies should be brought into closer correlation. Without turning aside from its chief end, which is the quest of understanding, science might be directed with greater determination towards the relief of man's estate. And the democratic tendency would gain if it could be more informed by knowledge, if it could acquire the habit of basing action, neither on prejudice nor on desire, but on the facts and the whole facts of the case.

Now one of the indispensable ideas which must be gripped is the idea of the web of life, the correlation of organisms, the linking together of vital interests in a Systema Naturae. This idea is essential to the scientific outlook on man and Nature; it is of incalculable practical importance, but it is also an idea as pleasant as the vision of light itself. It makes for delight as well as for discipline.

Let us try first of all to make the biological idea clear. No creature lives or dies to itself. Animate nature is a vast system of linkages. Gilbert White was aware of this when he wrote his famous letter (1777) on the influence of earthworms in the economy of Nature. Christian Conrad Sprengel was

on the same line of thought when he showed in his *Newly Discovered Secret of Nature* (1793) the intertwining of the lives of flowering plants and their pollinating insect-visitors. Many naturalists have had glimpses of the system of inter-relations, but it was Darwin who first discerned its subtlety and evolutionary importance and made the idea of the web of life *germinal*.

To vivify the conception of the web of life, and man's share in it, it is useful to think of particular types. Thus in his study of the work of earthworms Darwin showed how many other circles of life their life intersects. They make the earth suitable for plants and for man's agricultural operations; they bring bacteria for good and ill to the surface; they plant trees; they are preyed upon by carnivorous beetles, centipedes, birds, moles and so forth. Similarly, if we take white ants or termites, how many other circles their life-circle cuts. They prune trees and make alluvial soil; they grow fungi on labyrinthine beds and keep guest-beetles with a narcotic exudation; they wage war on true ants and are preyed upon by ant-eating mammals, birds and reptiles; they hinder the spread of civilisation by destroying posts and boxes, furniture and books. There are places, they say, where it is dangerous for a man with a wooden leg to go to sleep without special precautions.

Just as there is a correlation of organs in the body, the various parts being members one of another, so there is a correlation of organisms in the economy of Nature. Every one knows Darwin's cats and clover story, and how he once got eighty seeds to germinate from one clodlet from a bird's foot. A sparrow cannot fall to the ground without sending a throb through a wide circle. In the poet's fine hyperbole: "Thou canst not stir a flower without troubling of a star." There is a beautiful correlation between the amount of sunshine in spring and the supply of mackerel at Billingsgate. For as all flesh is grass, so all fish is infusorian and diatom and sea-grass. As Shelley wrote:

> Nothing in this world is single;
> All things by a law Divine
> In each other's being mingle!

As Locke said: "Things, however absolute and entire they seem in themselves, are but retainers to other parts of nature."

Fresh-water mussels cannot continue their race unless their young ones sojourn for a while attached to minnows and other fresh-water fishes; and the continental fish called the bitterling (*Rhodeus amarus*) cannot continue its race unless its young ones sojourn for a while inside the gill-plates of the fresh-water mussel.

But our subject is not the web of life throughout animate Nature; we wish to envisage the web of life as it affects man and his interests, or is in turn affected by him and them. Already, however, this is plain, that if animate Nature is in reality a vast interlinked system, the fact must be recognised in all possible detail by every one who would operate on Nature wisely, who would seek to control in any effective way the activities, structure, numbers and distribution of living creatures. If we are to control Nature, we must first know and then respect the intricacy of the web of life. By ignoring or defying it, man has brought much trouble upon the earth.

1. We may begin with man as a more or less deliberate distributor. It was thoughtlessly but not unconsciously that he introduced rabbits (about 1860) into Australia, with results nothing short of disastrous. It is true that millions are exported as food, but the damage remains. Partly in the hope of checking the elm-tree caterpillars, the European sparrow was introduced into Connecticut. This was done repeatedly. In some measure the sparrow checked the caterpillars, but only to become itself a greater pest, doing much damage to crops and driving away native insectivorous birds. It is also blamed for spreading among poultry certain diseases, such as "blackhead" due to parasitic coccidia. The mongoose introduced into Jamaica to exterminate rats fulfilled its mission, and then proceeded to exterminate poultry and ground birds, besides some useful insectivorous reptiles, some species of which have almost disappeared. Ground lizards of the genera Ameiva, Mabuia and Celestus have become scarce, and some snakes have suffered even more. The reduction

of the numbers of insectivorous birds and lizards has meant an increase of injurious insects, and so the influences spread like surface circles on a quiet stretch of the river.

2. Sometimes man's operations should be called encouraging certain forms of life, rather than directly extending their range. Thus, by considerable carelessness in the disposal of refuse or in neglecting to nip an evil in the bud, he has encouraged the multiplication of rats, which now cost Britain several million pounds every year. In some other countries it is worse; thus around one sugar-factory in Java between nine and twelve thousand rats were killed every day for several years. It is not only their destructiveness that is to be deplored, but there is serious risk involved in the fact that the rat harbours the Nematode parasite, *Trichinella spiralis*, which causes the disease of trichinosis in pig and in man, and in the fact that the rat-flea harbours the bacillus of bubonic plague. It has been said that plague is distinctly less frequent in those Indian villages that have plenty of cats. For the cat kills the rat.

Professor Fraser Harris has suggested that the emerods or haemorrhoids mentioned in the Book of Samuel (1 Samuel vi. 5) were the buboes or swellings of plague. Now this scourge is due to a bacillus, which also occurs in rats, mice and marmots, and man is usually infected by being bitten by a flea which has been feeding on a plague-stricken rodent. Professor Fraser Harris asks whether we may find in the five golden mice made on the recommendation of the Philistine soothsayers any glimpse of the fact that the over-running of the land with mice was not unconnected with the plague of emerods. He notes that "no rats, no plague" is an old saying amongst the people of India.

3. In yet other cases it must be admitted that man's disturbance of the balance has followed as the almost inevitable consequence of a laudable achievement. The potato-beetle or Colorado beetle (*Doryphora decemlineata*) was a native of the Central West of North America, where it fed on the deadly nightshade and was kept in check by natural enemies. The introduction of the potato plant (an ally of the nightshade)

and the extension of potato fields afforded an opportunity for prolific multiplication of beetles, and this the natural enemies were no longer able to check. Year after year the beetles extended their march westward till they reached the Atlantic seaboard. In spite of many counteractive measures, they continue to levy a very heavy toll.

It seemed laudable indeed to introduce European trout into Tasmanian streams, where they have prospered and been profitable. But there is always a tax to pay. The trout have been levying toll on the dragon-flies, and already, as Mr. Tillyard tells us, some characteristic Tasmanian species are becoming rare. A trout's stomach may be found crammed with over a score of dragon-flies. But dragon-flies live on insects which they catch on the wing, and many of these insects are injurious to crops and trees. So the introduction of trout into Tasmania means a tax on farmer and fruit-grower.

4. Now and again the disturbance may be traced to an unfortunate accident, as in the diagrammatic case of the gypsy moth (*Ocneria dispar*). About 1869 a French naturalist in Massachusetts, Trouvelot by name, had imported some specimens of this moth from Europe for some scientific purpose. Inadvertently, some of the caterpillars were allowed to escape, and although Trouvelot did all he could to avert the consequences of the accident, and did not delay in reporting it to the authorities, the gypsy moth caught on in the States, and, along with another introduction, the brown-tail moth (*Euproctis chrysorrhoea*), continues to do terribly destructive work in defoliating trees. Both are still unconquered pests.

Very suggestive of the "wheels within wheels" is the case of a scale-insect introduced into California along with some young lemon trees from Australia. It became a pernicious pest defying control, but was eventually mastered by importing from Australia one of its natural enemies, a lady-bug. The almost complete elimination of the scale left the lady-bugs to die in turn. Nowadays, "protected colonies of scale and lady-bug are kept in readiness to control future outbreaks of the pest." [1]

[1] Prof. R. S. Lull's *Organic Evolution* (1917), p. 111.

5 Let us look at some illustrations of the same sort of disturbance of the pattern of the web, but from the minus side, when man eliminates instead of fostering. Without pretending that this is the whole truth, we may safely say that the over-destruction of certain birds of prey, such as kestrels and owls, and of certain carnivores, such as weasels, is in part to blame for the occasional occurrence of vole-plagues, which turn fertile fields into deserts. Elimination in the interests of game-preserving is thus apt to be at the cost of the farmer. It seems likely enough that saving the red grouse from Nature's sifting is one of the radical conditions of an outbreak of so-called "grouse disease."

There is an Australian story which reads as if written for man's instruction. On certain Murray River swamps several species of cormorants used to swarm in thousands, but ruthless massacres, based on the supposition that the cormorants were spoiling the fishing, reduced them to hundreds. But the fishing did not improve; it grew worse. It was then discovered that the cormorants feed largely on crabs, eels and some other creatures which devour the spawn and fry of the desirable fishes. Thus the ignorant massacre of the cormorants made for the impoverishment, not for the improvement, of the fishing. The obvious moral is that man should get at the facts of the web of life before, not after, he has recourse to drastic measures of interference with the web of life.

It is not sentiment but science that warrants the strongest disapprobation of the careless destruction of birds. For the system of Nature depends on the check that birds keep on the multiplication of insects. Perhaps six years without birds would serve to bring our whole system of animate Nature to an end. The destruction of the beautiful white heron or egret for the sake of its scapular plumes has robbed nearly half the world of a bird of high utility to man. Its formerly abundant presence in the rice-fields of China and India is said to have been very beneficial: the bird has in great part fallen a victim to ignorant or ruthless fashion. There is but a short list of birds that are seriously injurious to the interests

of farmer and gardener; of a considerable number it must be said that while they do harm they also do good, and that the balance is in their favour; of the vast majority it may be safely said that they are beneficial. They are joys for ever besides.

The elimination of animals hostile to man or his interests is often agreed upon as beyond all question desirable, but there is very frequently a tax to pay. The extermination of poisonous snakes is probably inevitable, but one must at least be prepared for a multiplication of the mice and other "vermin" on which many of the snakes normally fed. In studying the influence of birds and other creatures on man's material interests, one is continually confronted with the difficulty of getting a "clear issue." Squirrels are destroyed because they spoil so many young trees; but the result is an over-multiplication of wood-pigeons, on whose young squabs the ordinarily vegetarian squirrel levies useful toll.

6. Without any active elimination man may bring about serious changes by what we may call discouraging certain types. Thus the gradual extension of arable land, the gradual paring away of the delightful wild corners, the drainage of swamps, the clearing of golf-courses, and so on, are having a rather dismal effect on our British fauna. Many interesting types have sought remoter retreats or have left us altogether, and the nemesis of cutting off the nesting-places of common insectivorous birds has made itself felt in many places. One hopes, however, that there is a fresh growth of a vivid and determined awareness that creatures like bitterns and badgers are national treasures of real value, not to be sacrificed any longer either to ignorance or greed.

7. Some of the most striking linkages are those concerned in various diseases of man and his stock. Malaria is due to a minute animal which lives in the red blood corpuscles of man; it passes into a mosquito (*Anopheles maculipennis*) that sucks man's blood; after complicated changes in the mosquito the microbe passes into the blood of another man whom the insect bites. As the larval mosquito lives in pools and breathes at the surface, it can be suffocated by a floating

film of paraffin ; or it will disappear if the pools are drained, or filled up, or poisoned. But is it not a fine instance of the web of life that the importation of top-minnows into infested waters is one of the surest ways of getting rid of mosquitoes and thus of malaria ? Eleven species of Indian fishes are of proved value as mosquito-destroyers, and some might well be used in city tanks.

Yellow fever is spread by another mosquito (*Stegomyia fasciata*); and the blood-worm (*Filaria bancrofti*), which causes elephantiasis, is carried by yet another. The young worms from the blood of a victim undergo changes in the interior of the mosquito's body, and the resulting forms pass to the proboscis, by which they are deposited on man's skin, into which they bore.

One of the important things to understand about parasites is that they very often do little or no harm to their wonted host; it is when they are passed into a new host that they spell disaster. Thus the microscopic animals (trypanosomes) which cause sleeping sickness in man, and its analogue in cattle and horses, seem to be at home in antelopes and reed-bucks, which are accustomed to them. When the tsetse flies sucking the infected blood are themselves infected, and transfer the trypanosomes by and by to man and his stock, then the mischief is done. For the blood of the new hosts has not the necessary anti-toxin to the formidable trypanosome. The whole riddle is not yet read, but we need it only as an illustration of a general fact, that the tsetse fly links antelope or some other wild reservoir of trypanosomes to man, and that the damage done is due to altering the existing arrangement of the threads in the web of life. That alterations have been necessary and will continue to be necessary as civilisation proceeds cannot be gainsaid ; the point is to realise what all such changes are likely to involve, and to bring all available science to bear on any proposed change, so that distant as well as immediate consequences may be, if possible, anticipated.

It may here be mentioned that the widespread belief that house-flies sometimes bite is due to the occasional presence

indoors of the blood-sucking "stable-fly" (*Stomoxys calcitrans*), in regard to which there is a strong suspicion that it may have something to do with carrying the infection of infantile paralysis.

Even flies which are not blood-suckers are important as distributors of disease-germs. That the common house-fly (*Musca domestica*) helps to spread the microbes of typhoid fever seems certain; and in regard to summer diarrhoea of infants, dysentery and cholera, the evidence is "very convincing, both circumstantially and experimentally, but still requires a critical attitude." [1]

For diffusing Egyptian ophthalmia and other eye-diseases the common house-fly and the lesser house-fly (*Fannia canicularis*) are probably in part responsible.

It is certain that the house-fly is a serious drag on the wheels of the chariot of civilisation, and that it is incumbent on man to find cleaner and thriftier ways of disposing of the manure and other refuse in which flies breed. "A crusade against flies must aim at prevention rather than destruction, and must be applied against the insects in the early stages of their existence. The injunction, 'Kill that fly,' implies a confession of failure in sanitation" (Buchanan).

We must not say more regarding insects as carriers of disease-organisms; every one knows that lice spread typhus, and there are sundry ticks which are deadly disseminators, as of "tick-fever" in man and "red-water" in cattle.

One of the great life-savers during these tragically destructive years has been Dr. Leiper, who discovered in Egypt the life-history of the formidable worm (*Schistosoma haematobium*) which causes the serious disease of bilharziasis in man. In some parts of Egypt this disease affects every third person, and as the tiny, free-swimming, juvenile stage of the worm usually enters through minute cracks in the skin, it is very difficult for people who have contact with unfiltered water to evade it. Dr. Leiper showed that part of the early life is passed in several fresh-water snails, so that a check to these will check the malady; and, moreover, that the free-

[1] See R. M. Buchanan, *Insects in Relation to Disease* (Glasgow, 1916).

swimming larva cannot survive in drawn water for more than forty-eight hours. Thus a simple preventive expedient is open.

Major Leiper was led to his discovery by knowing that the young stages of the Trematode worm (*Distomum hepaticum*), which causes the disease of liver-rot in sheep, are harboured inside the little fresh-water snail called *Limnaea truncatula*, common in most pools. The more drainage of pasture-land, the fewer pools, the fewer fresh-water snails, the less liver-rot in sheep. And we may make the idea of the web of life picturesque again by noticing that the water wagtail is very fond of the fresh-water snails, so there is a linkage between the preservation of water wagtails—national assets in any case—and the success of sheep-farming.

Parasitism is a bit of a knot, perhaps, in the web of life, but perhaps we look at it most reasonably when we see it as a particular mode of a universal tendency to inter-linkage. And it is interesting to note that just as a partnership may sink into parasitism, so a parasite may sometimes make good by becoming a partner. This is probably the case with the mycorhiza fungi on the roots of some trees, and the bacteria in the root-tubercles of leguminous plants. But let us change the subject.

8. Teachers would find it useful to look up the 1903 British Museum Report on Economic Zoology, in which Sir Ray Lankester clearly arranged the chief practical inter-relations between man and animals. There are (1) those captured for food and other products, from rabbit to oyster, from whitebait to whale ; (2) those bred for use, from cattle to bees, from silkworms to turkeys ; (3) those that help, from earthworms to flower-visiting insects ; (4) those that hinder, from snakes to mosquitoes ; (5) those that injure useful animals and plants, such as voles and scale-insects ; (6) those that spoil man's permanent products, such as white ants, clothes moths, book-worms, and (7) those that keep down the last three, from lapwings to lady-birds, from hedgehogs to ichneumon flies.

The mere statement of this useful classification suggests

many a piece of the web of life that means much to man. But we cannot enter into the large questions of domestication and utilisation.

In years to come a fundamental national need will be increased production of useful plants and animals. We know that this may be in part attained by working with prolific races, whether of wheat or of poultry, as Professor Punnett will explain in a subsequent lecture; we know also that many animals and plants which have not been utilised in the recent past might become valuable assets; we know also how the chemist by capturing the free nitrogen of the air can make fertilisers which facilitate intensive cultivation. But are there not what we may call web-of-life methods? Just as soil may be vastly improved by the work of leguminous plants—though they be mere weeds—with nitrogen-capturing partner-bacteria, so Professor Bottomley of this College has done more than suggest that bacteria may be used to liberate, as it were, the agricultural values of peat. Mr. H. G. Wells's vivid dream of a growing mixture is beginning to become real (like many other of his anticipations) in our knowledge of "auxetics" and "hormones."

In the quiet of the pond in the winter months there seems to be a preparation of growth-stimulants for the exuberant renascence of spring. But may there not be a miracle of fishes as well as of loaves? Here at least is a hint of one! Bundles of bracken thrown into fresh-water lochs seem to have promoted the vigour of the trout-population. Bacteria working on the bracken thrive and multiply, they afford food for Infusoria and they also liberate the stimulants of vegetative growth. The replenished hosts of Infusoria and Algae are devoured by minute Crustacea, which afford food for fresh-water fishes. Here we have a hint of a possible correlation between bracken and breakfast. And while the sceptic and patriot may refuse to cast his bread on the waters, who would not cast bracken, which is conquering all too easily in the struggle for existence with much better plants?

Much may be done in increasing productivity; much may

be done by reducing wastage. Thus there is room for a great development of bee-keeping in Britain, for bees collect large quantities of food which would otherwise be lost. They are able to feed themselves and yet produce much honey for us. We cannot look at a vigorous hive in summer without being impressed with the commonplace that the busy creatures are storing up energy for us in their honey, and yet asking nothing from us. The feeding of bees with sugar is modern and probably deleterious. The inter-linking of man and bees and flowers is a fine instance of the web of life; but there is an unfortunate knot—Isle of Wight bee-disease—which has wrought havoc among bees in Britain and elsewhere. But there is good reason to believe that the knot will soon be disentangled.

We hope that there are few able-minded people who will regard the illustrations we have given of man's share in the web of life as "diversions of natural history." It is really far otherwise. If we are to persist and advance in civilisation, we must pay more heed to the web of life, to all the queer junctions in our lines of communications. We cannot play the game without observing the rules, and the rules include a recognition of the web of life. We are parts of a system. Pressing hard and inconsiderately to a practical end may mean temporary victory and final defeat. Nothing lives or dies to itself. It is not the first nor the second consequence of a move that counts, but the sum of consequences.

But there is something more valuable to be gathered from our study than a conviction of the practical importance of the web of life; there is the suggestion that this way of looking at things is the accurate, the scientific way, and that it must dominate us when we are investigating the affairs of men. We should try to acquire as a habit of mind the vision of the web of life. For while we are part of the great Systema Naturae, bound to it by linkages which we have been considering, we are also a kingdom among ourselves, bound together in mutual dependence and influence in infinitely complex ways. There can be no permanently sound social action which does not recognise our solidarity,

and the multiplicity of consequences flowing from every change.

One of the many significant documents that have appeared of late is the Labour Party's draft report on reconstruction. While there is much in it with which many will disagree, there are some wise words that will command general assent. "Good Will without Knowledge is Warmth without Light. Especially in all the complexities of politics, in the still undeveloped Science of Society, the Labour Party stands for increased study, for the deliberate organisation of research, and for a much more rapid dissemination among the whole people of all the science that exists." That is well said; it sounds like the New Earth if not the New Heavens; but may we not plead that the science be science interpenetrated by the fundamental biological idea of the web of life?

The theory of Organic Evolution is still being evolved; it bristles with unsolved problems; all its propositions are crowded with difficulties. But some of the difficulties are not so formidable as they look. The central idea of Darwinism is the Natural Selection idea, that there is in the course of Nature a continual sifting or criticism of the novelties that well forth, the relatively less fit to the given conditions being in the long run, or in the short run, eliminated. To many naturalists the evidence of this discriminate elimination seems strong. But, it is often asked, how could the sifting and singling operate on little finicking details, which are so characteristic of living creatures? To this very reasonable question Darwin himself gave the answer by the emphasis he laid on the web of life. For in the gradually evolved and ever complexified system of inter-relations there is a sieve of extraordinary delicacy, which discriminates between even minute variations to the plus or minus side. Not that a slight disadvantage in a particular direction need mean "off with his head"; there is in the subtle struggle for existence a principle of compensations; a decision may waver for a millennium, and it may take another millennium of slightly smaller and slightly handicapped families to bring the relatively less fit to the vanishing point.

Another of the many difficulties raised by the evolution-theory is to account for the general progressiveness of the process. There have been blind-alleys, retrogressions, lost races and so forth, but on the whole life has been slowly creeping upwards. Evolution makes for progressive integration. But why should it? Is it not worth considering whether part of the answer may not be found in the gradual complexifying of the web of life? There is established an external system of inter-relations which is always becoming more intricate, and this forms the sieve by which variations are sifted. There has been an evolution of sieves which partly account for the progressive evolution of the sifted.

Finally, this suggestion arises from our study. The kingdom of man is very different from the realm of organisms, and no one will wisely argue from animals to men without careful verification. Now, one of the great differences is that in mankind the external registration of racial gains is of paramount importance. Language, literature, laws, traditions, institutions and so forth mean so much. But in part these correspond to the external systematisation of inter-relations which we call the "web of life"; the rest of the counterpart being discoverable in all the multitudinous inter-relations which bind men together in dynamic correlation. If so, how carefully we should study all the social inter-relations; how carefully we should scrutinise them in the light of evolutionary ideals—for they form a sieve for variations and it is idle to think that human society can persist or progress without siftings to take the place of the natural selection now so largely superseded; how carefully we should seek to reduce what might be called mutual inhibitions and to increase those inter-relations by which we provoke one another to good works. How important for our national future, for civilisation's future, is the improvement of the pattern of the human web of life, and the only way to effect that is actively to enter into new combinations with noble purpose. Thus we evolve our own sieves, separating chaff from wheat.

I cannot think that it is other than accurately scientific to

discern in Nature a tendency to complexify, to correlate, to interlink, to federate, to establish a dynamic system of interrelations, to work out an organic solidarity; and that this is part of Nature's message to man. Does not the Web of Life which we have been studying point on to a League of Nations?

V

THE ORIGIN OF MAN

By F. WOOD JONES, M.B., D.Sc.
Professor of Anatomy in the University of London.

V

THE ORIGIN OF MAN

YOU will, I am sure, forgive me if I strip from this lecture all pretence of polite introduction, since the subject allotted to me in this series is one which cannot be dismissed in the course of an hour's lecture even when only one very limited aspect of the question is passed under review.

The problem of man's origin touches at so many points a wide series of separated sciences. Evidence is to be derived from the study of ethnology, of palaeontology, and other cognate sciences, and important though this evidence is it cannot properly be analysed in so brief a time; even the evidence to be derived from a study of the structure of Man, which is the only aspect of the problem with which I shall deal, cannot be put before you in even its most meagre outlines unless we are prepared to discard all those ornaments which are regarded as properly belonging to a public lecture.

I have no new theory to put forward concerning this problem, no new views to advocate, I have even no new facts to record; but nevertheless I have a very definite purpose in giving this lecture.

These are times when long-cherished ideas, and long-accepted theories, are easily (perhaps at times rather too easily) placed in the melting-pot, and although I am not going to ask any one to sacrifice ideas to which he has long been reconciled, I would urge that the question of the origin of Man is certainly one concerning which it is legitimate to ask if the foundations of our teaching are sound. The evolution of Man is a fascinating problem; but the evolution of our ideas

concerning the zoological position of Man forms a study but little inferior in interest, and one that must be followed before we can rightly appreciate the position of the problem to-day. I would say that, as an introduction to any research work, it is essential that the worker should realise how the atmosphere of thought, wherein he was reared, came to be formed about his subject. It is essential to know how we slid into, or how we were forced into, the opinions we hold to-day. With regard to the zoological position of Man it is, I think, correct to say that in part we have been pushed, and in part we have slid, into our present opinions.

It is this aspect of the question that I wish to outline very briefly to you.

Over 300 years before the Christian era Aristotle had started upon the never-ending work of classifying animal forms. We may picture how any pioneer of this enterprise would have set about his business. He would have started, beyond a doubt, by setting side by side in his scheme those animals which appeared to him to be most alike; the whole psychology of the systematist, whether he lived 300 B.C. or in A.D. 1918, demands a classification by likeness to form the basis of any ordered arrangement. Order is created only by the adoption of such a method. But something more than mere order is achieved at the same time, for the assumption that likeness implies kinship is a very natural one. Man is so accustomed to observing likeness between related forms, that it is but natural for him to regard very similar forms as being nearly related to each other. From Aristotle to Linnaeus is a passage of 2000 years, and in the passing of this time great strides have been made in classification: every known member of the animal kingdom has been put into its appropriate place, and the result is an ordered array of animals classified by their likenesses, their likenesses always being regarded as an expression of their kinship.

Similarity of form has ever demanded proximity in the scale, and similarity in common experience argues relationship. But even the earliest of the systematists (and to Aristotle this credit must certainly be given) saw that something beyond

mere order and kinship was expressed in schemes of classification. It was obvious that some forms were simpler, less organised, "lower" than others, while some were obviously "higher" and more nearly akin to Man, and it only required the completion of a scheme of classification to light up the alluring concept of the "Scale of Life." This is a definite stage, and an important one, in the evolution of our ideas. In 1643 Sir Thomas Browne caught the notion and termed it the "stair or manifest scale of creatures rising not disorderly or in confusion." Edward Tyson, the anatomist, in 1699 dealt boldly with the idea, and placed his chimpanzee upon a stair above the monkey, and Man a stair higher than the chimpanzee, and then to round off the whole he placed the angel on the step next above.

Charles Bonnet, in 1750, elaborated the idea to its utmost and included all naturally occurring objects, animal, vegetable and mineral, within this glorified *échelle des êtres*. Charles White of Manchester published it in 1799 under the guise of "regular gradations." In his "gradations" Charles White placed the negro definitely below the white man, and gave him the position of a transition form between the monkey and the European. For England this was to seal the fate of the work; for just at that time any attempt to lower the zoological position of the negro was to run counter to the anti-slavery agitations on behalf of the African, and White's book was a failure so far as concerns the progress of thought.

But in France the idea was destined to grow, and in its growth it took on a newer phase. The French zoologists recognised how little was the difference between two neighbouring animals in the scale, how little was the modification that marked one step above or one step below, how stable was the underlying basal type, how infinitely subtle its minute modifications. There was, as the phrase of the time had it, "a unity in variety" not unlike the conception of Plato of "a unity of design," and this trend of thought was crystallised by the saying of Étienne Geoffroy that "philosophically there is only a single animal." From France the idea returned to England, and under the guidance of Robert Knox, the

anatomist, became the creed of the so-called "transcendental school" of Anatomy. It is hardly necessary to trace in any detail the most elaborate product of this line of thought. Less subtle minds seized upon the idea of "unity in variety" and sought to define exactly in what that unity consisted. A German school (Goethe, Oken, Spix, Carus) laid the foundation of that concept which grew to be a nightmare, and which we may dismiss as the conception of the "Archaetype." From the early years of the nineteenth century till 1859 the Archaetype grew to gigantic proportions. But in 1859 it fell with a crash. In 1859 Darwin's views became the dominant note in current thought, and the Archaetype was forgotten.

It is useless to consider Darwin's work apart from the atmosphere of thought into which it was launched. Classification by likeness was established, the scale of life was familiar, the stability of the basal type was recognised, the minute variations which separated step from step were appreciated. Even the conception that step could change to step had entered the minds of many, and the fixity of species was the subject of academic debate. In a way that is very remarkable, but which is nevertheless true, Darwin suddenly opened the eyes of mankind by showing, as a practical proposition, how step did change to step, and that the scale of life was a moving scale.

No matter what the reservations of the thinking few may have been, it is just to say that for most men Darwin animated the scale of being; he showed it as a living, moving procession towards perfection, the lowest at one end, the highest at the other, but all moving onwards, all evolving. Such a conception of a uniserial march of progress might be termed "end on" evolution, and as such I shall brand it.

What has been the fate of "end on" evolution as a theory? The lower end of the scale of being has in these days of specialisation of learning been left to the biologist. Wherever his patient labours have been pushed home he has played havoc with the uniserial march of progress. Some expressions of Professor Dendy, during his introductory lecture to this course, will linger with those of you who were present, and there is no

need to recapitulate the biologist's finding that the highest members of the group below do not in general become the ancestors of the lowest members of the groups above. I need only instance the case of the much-debated question of the origin of the vertebrates. Did their lower members arise from the highest of the invertebrates, which stand immediately below them in the scale of life? To my mind the work of the late Richard Assheton makes it perfectly clear that there is no meeting-point of vertebrate and invertebrate nearer than the Coelenterata. It was not that the highest invertebrates became the progenitors of the vertebrates, but that the two stocks arose in common from so simple a form of life as the hydra, and branched off, each along the line to which its definite structural bias had committed it. The middle portion of the scale of life has afforded an object of special study for the zoologist and the palaeontologist. Here, again, all the evidence gained from patient researches upon the phylogeny of the main groups of the vertebrates has altogether discredited any belief in "end on" evolution. Multiserial evolution, by which many stocks arise and diverge along their own line, is the order of development, rather than the transition of one group into its next higher neighbour. To take a very obvious example, it is not the highest reptile, not the most perfected expression of reptilian development, that leads the way to the lowest member of the group above, but the lowest reptile, the least developed and differentiated member of its phylum, which makes a bond with other phyla. We have a series of evolving lines, and no march of progress to perfection along a single line.

If, then, such are the findings of those who have patiently investigated the lower end, and the middle, of the scale of being, what conclusions have been arrived at by those who have investigated its immediate culmination in the highest order of the mammals?

So far as influencing opinion is concerned, it is safe to say that the examination of the highest rungs of the scale remained in the hands of Huxley and Haeckel in that stormy epoch of the immediate post-Darwinian period. Of their findings there

can be no doubt; they both belonged to the school which may be termed "the school which saw no difficulties"; and it is against the uncritical acceptance of the teachings of this school that I wish to raise a caution. I alluded to a purpose underlying the delivery of this lecture, and that purpose is to point out to you the dangerously easy slide which opinion has made after the extremely vigorous push administered in the past half-century by Huxley and Haeckel.

Haeckel divided the sequence of evolution into stages. In the 21st stage evolution attained the status of the lemurs: in the 22nd stage it had passed on to the New World monkeys: in the 23rd the stage of the Old World monkeys was reached: in the 24th the anthropoid apes had been developed. Pithecanthropus, the Javanese "missing link" of Dubois, unearthed at Trinil, was the representative of the 25th stage, and Man was easily attained in the 26th. To this simple declaration Haeckel attached "absolute certainty," and to make his position clear he represented the stages graphically as a linear series of developmental steps! That was an easy scheme to grasp, an easy statement for the general public to swallow whole, especially when it was backed by the weight of the authority of a learned German professor.

Huxley worked on rather different lines. He took a dictum which was first enunciated by Buffon, and was already a hundred years old, and he elaborated it into a thesis which took the published form of *Man's Place in Nature*. This work exercised great influence, and is of the first importance in any inquiry into the formation of our present ideas concerning the origin of Man. Buffon had said of the orang utan that "as regards his body, he differs less from Man than he does from other Animals which are still called Apes." Huxley took this as his thesis, and made it his creed. Haeckel received this hundred-years-old dictum with acclaim, and he termed it the "Huxleyean Law" or the "Pithecometra thesis." Haeckel lived under the delusion that to give a name to a process was to imply an understanding of the process, and this name has acted as a talisman ever since.

Huxley was a man of far more mental subtlety than

Haeckel, but there is no doubt that he regarded an "end on" evolution as being the sequence of progress in the culmination of the scale of life. He it was who looked for a "missing link" between Man and the existing anthropoid apes.

The influence of these two men has gone far, and it is necessary to see how much our ideas to-day are dependent upon their published works. Haeckel may be said to have shouted, with brutal directness and with raucous voice, the message that Man's origin from lower forms had been definitely proved to pass in its later stages through the lemurs, monkeys and anthropoids. There were no half-tones, no doubts for this man: he attacked with an unfailing discourtesy all who stood in his path. His reputation was European and for Europe he did this disservice, that he shouted down opposition, and that, armed with these assumptions, he deluded the masses, as he deluded himself, into believing that his flimsy and hastily drawn speculations were the bed-rock certainty of carefully sifted, specialised knowledge.

Huxley was by instinct a fighter and an educationalist, and for England he very largely helped to mould the trend of research into this, the culminating end of the scale of life. With his century-old dictum he impressed a very wide circle, and he laid the foundation of research in seeking for likenesses between the members of the Primates. He sought to demonstrate the likeness of Man to the anthropoids and to make apparent the steadily decreasing likeness as the sequence was followed back through the monkeys to the lemurs. It was perhaps Huxley's demerit that he either did not look for, or easily smoothed over, differences. He did not analyse; he did not critically weigh likeness against difference; he brushed aside difference and magnified likeness. Working along these lines he showed that Man was very like the anthropoid apes, and they in their turn were like the monkeys, which resembled the lemurs. He and Haeckel were the most influential apostles of the school which saw no difficulties in the origin of Man from the anthropoid apes *via* the monkeys. The influence that Huxley exercised in England has lived after him, for it is to-day the accepted method of investigation that

the origin of a human characteristic be sought first in the anthropoids, then in the monkeys and lemurs, and afterwards in a "lower," pronograde mammal. The following of this line of investigation has led to the production of some extraordinary nonsense.

It is natural to ask if there were no dissentient voices raised against the trend of thought which saw no difficulties in the path of "end on" evolution in the culmination of the scale of life. As a matter of fact there were many, but they produced but little effect upon the rising tide of thought; and it is fair to say that the idea of Man's immediate origin from the existing Primate series, which was so repugnant to many when first enunciated, gradually became familiar, and in the end was accepted without question by the majority of mankind. Such a progress seems to be typical; for when once opinion has been rudely shocked and has subsequently become anaesthetic and reconciled, it will swallow the disturbing theory without hesitation; it would indeed rather hug it in blind faith than face another disturbance of ideas. We all became reconciled to the belief that we were the perfected product of the "end on" evolution of the Primates, that the anthropoid apes were our immediate ancestors, and that behind them stood the evolutionary gradations of Old World monkeys, New World monkeys and lemurs. That is the position into which we were first hustled and into which we have since quietly drifted.

Since the time of Huxley and Haeckel the study of the highest steps of the scale of life has fallen, for the most part, upon the shoulders of the human anatomist, and it must be owned that the burden has sat but lightly upon this already overworked individual. A more fitting recipient of the mantle would have been the comparative anatomist; but it is our misfortune that we have to own that, in our own country at any rate, the comparative anatomist has not given himself greatly to the consideration of this problem. Richard Owen was England's comparative anatomist during the Darwinian period, and there is no need to recall those bitter times of his dying effort to stem the tide. Mivart may be regarded as his

successor, and he fared no better, though he deserved rather more. Neither Owen nor (later on) Mivart was content to stand by and see the triumphs of a school which regarded likeness between Man and the anthropoids as all-important and yet totally disregarded the obvious differences which separated them. Owen was defeated, Mivart was a voice unheeded, yet both worked honestly and in the interests of truth, rather than in the interests of a popular movement. Their fate was the same. The public had been educated. They had come to regard the origin of Man from the existing anthropoids as a settled fact, and having taken this decision after a period of painful disturbance, they were not going to permit an upset of their newly acquired creed.

It is not to be presumed that we may speak with a tongue so persuasive and so logically incisive as that of Huxley, nor in a voice so dominant and raucous as that of Haeckel —nevertheless the time is now ripe for a school of thought to proclaim itself as being one that insists upon the recognition of differences as well as upon the institution of likenesses. It is not alone that we are passing through a period when the recasting of opinion might perhaps be more readily effected; it is not because we are living in a time which maybe owes its troubles in part to the easy acceptance of the creed of 1859; but rather because the school which sees no difficulties is gaining added strength from the work of certain palaeontologists that I have deemed it timely to deliver this lecture. The palaeontologist has to be satisfied with the examination of very sparse remains of extinct animals; he cannot, of necessity, study the viscera, the muscles, the nerves, or in many cases the structural details of cranial architecture. He is forced back, in most cases, to the study of fragments of the skeleton and the more or less perfect remains of teeth. From the examination of such fragments it is all too easy to assume that the readjustment of the cusps of a molar tooth here or there will turn some fossil precursor of a chimpanzee into the extinct precursor of a Man. But Man differs from the anthropoids in so many more details of structure than those that can ever be available to the palaeontologist, that

it may be well to raise a voice—though maybe a feeble one —against the ready acceptance of this, the newest departure of the school which sees only an easy gradation from the monkey to the ape and thence to Man.

One other point demands attention. It must be remembered that when Darwin's work was published, and when opinion was being recast so hurriedly, there was but little appreciation of those marvellous adaptations of animal structure by which creatures living similar lives become modified along similar lines. This is the phenomenon known as convergence, and we know quite well how wonderfully animals of utterly different stocks may come to resemble each other in a host of superficial features. The undoubted action of such a factor should ever be present in the mind of any one who would attempt a classification by likenesses which has any pretence to represent genetic relationship.

We will therefore attempt to apply two cautions in studying the presumed immediate ancestors of Man, the first that we do not overlook differences when we find them, and the second that we do not overrate likenesses which may be due to nothing more than similarity of adaptation in animals living in similar environments.

The immediate ancestors of Man constitute the group known as the Primates, and this group contains what Haeckel and others have conceived to be a phylogenetic series composed of (1) the lemurs or Strepsorrhini, (2) the Tarsii, (3) the New World monkeys or Platyrrhini, (4) the Old World monkeys or Catarrhini, (5) the anthropoid apes, and (6) Man. The position of the lemurs with regard to the rest of the families constituting the order has been frequently debated. Without entering into details, I shall have to be content with the mere statement that in all parts of their bodily structure lemurs show so many, and such deep-seated, differences from the Anthropoidea or monkeys, that the value of the trivial and superficial likenesses is far outweighed. When the whole anatomy of the lemurs is taken into account it becomes apparent that they are severed so sharply from the rest of the Primates that their retention within this order seems

undesirable. The lemurs are a primitive set of Eutherian mammals; and that they are an ancient stock is well known, since Pelycodus, Adapis and Notharctus of the Eocene are practically identical with the living forms. But that they are in any sense the ancestors of the Anthropoidea is highly improbable.

It must not be forgotten that, living in the same geological epoch, and even at an earlier period, were the curious forms known as Anaptomorphus and Necrolemur. The importance of these two forms in the study of the origin of Man is difficult to overestimate; but it is likely to remain unappreciated so long as Tarsius, their living descendant—almost their living picture—is regarded as nothing more than a somewhat specialised lemur. Tarsius is a most curious little animal; but he is a little monkey and not a lemur, and Anaptomorphus of the Eocene of Western Europe and North America may, judging from the skeletal likenesses, safely be assumed to have possessed all, or most, of those features of the perishable parts of the body which stamp it so distinctly as a primitive, though specialised, member of the Anthropoidea.

To discuss the inter-relations of the Tarsii, the Platyrrhini and the Catarrhini is too far-reaching an inquiry to embark on within the limits of this lecture, and it will merely be possible to call attention to a few points which bear most directly upon the problem immediately before us. Where does Man stand in the group of the Anthropoidea as thus constituted, and how does he differ from the other members of the group? Since this is a cautionary lecture I will first select a point which, though adaptive and probably not of extreme importance in determining genetic affinities, is one that will serve to bring home to you the line of thought I am attempting to follow.

Galen, who laid the foundation of so much of our knowledge of Anatomy, was very much better acquainted with the structure of the monkeys and lower animals than he was with that of Man. It is notorious that when he described the anatomy of Man he filled in all the blanks of his knowledge with facts gained from dissections of lower animals. In this way he led men to believe that as a part of the normal structure

of the skeleton of the face there were two separate bones, bearing the incisor teeth and marked off from the maxillae by suture lines such as are present in monkeys. The great Vesalius in 1543 showed that this facial suture line did not exist in Man, although upon the palate the line which separated the os incisivum from the maxillae was conspicuous. It was useless for the adversaries of Vesalius to urge that though the suture might be absent in the degenerated men of the time it was certainly there in Galen's day. Others were ready to affirm its universal absence. Camper was probably the first to claim that the absence of the separation of this element was a distinctly human characteristic. Blumenbach followed him, and named the bone in question the intermaxillary. Sir William Lawrence laid especial emphasis upon what he regarded as the entire absence in Man of this bone, now generally known as the premaxilla, and he insisted that it separated Man from all other animals. It is true that, as was shown in 1699 by Edward Tyson, the suture line disappears in the adult chimpanzee, and, as Daubenton showed later, in the orang utan, but, nevertheless, the facial separation of the premaxilla element is marked in younger specimens.

This question of the curious isolation of Man in regard to this feature bulked fairly large in the anthropological literature of pre-Darwinian times. How was it regarded by those who saw in the times immediately following Darwin a ready transition from monkey to Man? There is no doubt as to the answer here—it was ignored; in the scramble for likeness such an inconvenient point was dropped out of consideration altogether. Our modern text-books of human anatomy give the student remarkably little help in this matter, and the question of the facial portion of the premaxilla cannot be said to be thrust upon their notice. And yet some attempt must be made to bridge the gap which here separates Man from the monkeys.

Since Man is regarded as the immediate descendant of the anthropoid apes, the loss of the individuality of this element should be recent in the story of the race and therefore late in the development of the individual. It has been shouted even

into the streets that every developing individual recapitulates the story of his race—that he climbs his own ancestral tree. It is obviously out of regard to this dictum that our text-books sometimes lull the student's propensity to inquire by vague statements that traces of the facial suture lines are commonly present in the human skull at birth. It must also have been in some such way that the distinguished author of the Cartwright Lectures of 1892 told his audience that the human premaxilla is sometimes partially and sometimes, but more rarely, wholly isolated, and that it is late to unite with the maxillary in Australians, and in some examples of New Caledonians and Greenlanders. It is strange that we have not yet been told the actual facial articulations of this separate human premaxilla; for these articulations differ widely in the different groups of monkeys, and it would be extremely interesting to know them in Homo.

Now the actual facts of the case are very different; for it is only at its very first appearance as a cartilaginous nucleus that the premaxilla is separated from the nucleus of the facial part of the cartilaginous human maxilla. When the human embryo is no more than 19 mm. long—that is, about ten times the diameter of an ordinary pin's head—the premaxilla is losing its identity in the cartilage of the maxilla, and when the embryo is another 5 millimetres longer it has ceased to exist as a separate entity on the face. The process by which the facial portion of the premaxilla becomes lost as a separate element is a complicated one, and it involves far more than the mere loss of a superficial suture line, for the whole method of growth of this part of the face is involved. The human premaxilla is lost in, and becomes overgrown by, the facial portion of the maxilla, but it still shows its independence of the maxilla, not only upon the palate but within the nasal chambers. How very different a story is this from what Haeckel would have had us believe. We have been told by him that the developing human embryo could not be distinguished from the embryo of an anthropoid ape until the fourth or fifth month of pregnancy. Yet here is a detail which is absolutely diagnostic of Homo as a

zoological type, definitely established at a period in which the embryo was held to display perfectly generalised mammalian characters.

A host of other features in the skull present themselves in the train of this question of the premaxillary bone. In Man the nasal bones remain separate, as a rule, throughout life, but in monkeys and anthropoid apes they are greatly reduced elements, and they are frequently fused together into a single bone before the animal is born. In this very characteristic feature Man is considerably more primitive than are the monkeys. Again, the bones which form the floor of the cavity of the skull show a strange contrast as between Homo and all, save two, representatives of the Anthropoidea, for whereas in Man the primitive arrangement, by which the mesethmoid articulates on the floor of the skull with the pre- and orbito-sphenoid, is universal, in the monkeys and anthropoid apes a large bilateral ingrowth of the frontals separates these two elements. The arrangement of the bones of the cranial wall at the point known as the pterion is a more complex problem, but nevertheless it constitutes a distinction between the human and monkey skull which cannot be ignored, even if its significance is so far rather uncertain; and here again the human type is the simpler and more primitive one. Again, the late persistence, and not infrequent permanent persistence, of the separation of the two frontal bones at the metopic suture is a human feature which is not shared by the monkeys or anthropoid apes. Many authorities regard the human persistence of the metopic suture as a secondary feature re-acquired under especially human conditions of brain development. This may indeed be the case; but it is at any rate a primitive mammalian feature, and since so many such features are present in the human skull, and serve to distinguish it from that of the monkeys and apes, good proof of its secondary nature is needed for the acceptance of this belief.

Passing over many far less conspicuous, but still by no means unimportant points in which the human skull differs from that of the rest of the Primates, we may note one other

feature of the skeleton. The occasional existence of a supracondyloid spur, and even a supracondyloid foramen, in the humerus is a well-known anomaly in Man: it is not a common variation, and yet the spur is so uniform in its manifestations and in its peculiar relation to the brachial artery and median nerve, that it is obviously a true reversionary or atavistic variation. But none of the anthropoids or of the Old World monkeys have this spur or foramen as a normal structure, nor has it, I believe, ever been recorded in any of them as an anomaly. On the other hand, it is a well-known generalised reptilian and primitive mammalian possession. It is present in generalised Marsupials, Carnivora, Insectivora, Lemurs and American Monkeys, but it is absent altogether in those Primates which are reckoned as the immediate ancestors of Man.

In dealing with the far more plastic muscular system great caution is necessary to ensure that the results of dissections of the members of the Primate series convey any proper picture of the distinctions of Man. If all the variations that have ever been recorded in all the anthropoid apes be grouped together into one composite picture, then it must be admitted that there are singularly few muscular distinctions that can be claimed for Homo, when all the muscular anomalies that have been recorded in him are so blended as to form a complex human picture for contrast. On the whole, the total range of variations of the muscular system of Man very closely resembles that of the chimpanzee, and yet the average human subject differs from the majority of chimpanzees (1) by lacking certain specialisations which characterise the anthropoids, (2) by retaining certain very primitive features with great constancy, (3) by exhibiting certain definite human specialisations not present in the anthropoids. The second and third groups are those of most interest from the point of view of the origin of Man. We may note that the constant human retention of the ulnar fascia of the biceps cubiti is a primitive feature, lost in all other members of the Primates. Again, we may point to the normal presence of the primitive pyramidalis and the deep head of the pronator radii teres,

which make only an occasional appearance in the rest of the Primates. The insertion of the human pectoralis minor to the coracoid process is, contrary to the usual teaching, a feature in which Man shows a more primitive arrangement than that seen in any of the Primates except the anthropoids. As human specialisations we may note the presence of the peroneus tertius, the plantaris and the serratus posticus inferior, and again we cannot fail to be astonished at the remarkably early differentiation in the embryo of such a distinctly human character as the peroneus tertius. Of Primate specialisations not normally developed in Man we may cite the acromio-trachelian and the dorsi-epitrochlean muscles.

Of these muscles the pectoralis minor, the deep head of the pronator radii teres, the pyramidalis, and several others, are of particular interest, since, when Man more nearly resembles the anthropoids and differs more widely from the lower Primates, it is in the display of primitive features, which are lost in the monkeys, retained occasionally in the anthropoids, and preserved as normal features in Man. This is a point which needs particular emphasis; for the great bulk of the teaching concerning such structures has been formulated along the lines which were laid down by Huxley and to which I have already referred. If, upon these lines, the phylogeny of such a muscle as the pectoralis minor is sought, the human condition is contrasted with that of the anthropoid, and this in turn with that of the monkeys and lemurs, and this again with the arrangement present in a typical quadrupedal lower mammal. In this sequence a steady gradation is often displayed, and by orthodox teaching we are led to believe that the human condition is the more specialised—that it is the outcome of evolutionary stages seen in the making in the bodies of the animals examined. But one needs to go deeper than this, and to seek the muscle in the more generalised reptiles, in the Prototheria, and generalised Metatheria. When this is done a very different picture presents itself; for we find that the human condition is most primitive, that the anthropoid apes retain at times a nearly

equal simplicity, that primitive conditions are more widely departed from in the monkeys, and are finally lost by new adaptations in such specialised quadrupeds as the Ungulates. Far from the human condition being the last perfected specialisation it is, in these cases, the most primitive and least specialised type, from which the other forms have diverged in different directions.

In the vascular system the same story is unfolded. The arrangement of the vessels of the aortic arch in Man is exactly the same as that in Ornithorhynchus, and for many reasons it must be regarded as singularly primitive. The anthropoid apes at times retain this primitive form, but at others they are modified in the manner of the monkeys—a modification which is carried to greater lengths in the typical specialised quadrupeds. In those instances in which the peripheral vessels of the other Primates differ markedly from the typical human plan it will be found that the human form is the least specialised. This applies to such characteristically simian vessels as the arteria saphaena, which is certainly not a primitive blood-vessel of the leg.

Despite the wonderful rôle it performs in the function of speech, the human tongue is in structure a remarkably primitive organ, which differs widely from that which is typical of the monkeys. The tongue of the chimpanzee approaches very near to the human type, and were it not that the tongues of undoubtedly primitive mammals are ready for comparison, it would be easy to assume that the tongues of the chimpanzee and Man were specialisations of the condition seen in lower monkeys; when as a matter of fact the very reverse is actually true. The case of the tongue is particularly instructive in the study of the origin of minor anatomical details, since the two small sublingual folds (plica fimbriata and plica sublingualis), which are relatively extremely well developed in Man and the chimpanzee, are singularly like the same structures in certain lowly mammals. But while the American monkeys depart from such a condition in one direction, by the retention of the plica fimbriata, the Old World monkeys are specialised in the other, by the retention of the plica sublingualis. The

condition of these sublingual folds in the great divisions of the Primates would seem to point to the fact that the point of departure of the Platyrrhini and Catarrhini must have been from some very early form in which both folds were present—as they are in Man, the chimpanzee and Tarsius.

Strong confirmation of the evolution of Man *via* the systematic chain of the whole of the Primates is held to be evinced in the well-known condition of the human appendix caeci. The human caecum and appendix show a very striking likeness to the same structures in the gorilla, chimpanzee and orang utan, and this condition is usually regarded as being one of reduction and atrophy from the much larger organ of the monkeys and lemurs. The many considerations of diet, and the general uncertainty as to the precise nature and function of this portion of the bowel, render dogmatism in any direction a risky thing. Perhaps we do not know what the primitive picture of the mammalian appendix caeci is like, but at any rate we can make a comparison of the human condition with that seen in the Ornithorhynchus and Echidna. Here, again, we are faced with the remarkable fact that the similarity between the highest mammal and the lowest is very great, and, more than this, the appendix of Man is almost exactly paralleled in the Marsupial Wombat (Phascolomys), though it differs so remarkably from anything seen in the monkeys either of the Old World or the New.

The human kidney differs markedly from the type common to all the Old World monkeys and anthropoid apes, although at times the gorilla varies somewhat in the human direction. The New World monkeys, though differing from the Old World monkeys and Man in so many basal features, yet possess a kidney that is constructed definitely upon human lines.

In the reproductive system the presence of the hymen has been claimed from the very earliest times as a human distinction—a distinction which separated Homo not only from apes and monkeys, but from all the mammals. It is a distinction that one who insisted upon distinctions would be ready enough to claim but for the knowledge that a hymen is, in all prob-

ability, the common possession of the females of all mammals. It is almost pathetic that the one human distinction upon which all authorities are agreed, the one around which so many interesting theories have centred, and to which a peculiar literature attaches, should be the very one which must be cast aside as untenable. But one other remains, and this is a detail to which far less attention has been devoted. The human penis is perhaps the very simplest expression of a male copulatory organ to be found anywhere in the mammalian phylum ; it differs very remarkably in general form from that typical of the monkeys and anthropoid apes ; and the fact that no os penis, and no trace of cartilage, are formed in it at any phase of its development severs it utterly from the corresponding organ in all the Primates save Tarsius.

We must content ourselves with this as the sum of our brief outline of the story of the structural distinctions of Homo, and it has ended on a note which merits especial attention. Tarsius, alone among the Primates, resembles Man in having no cartilage or bone developed in the penis. Tarsius resembles Man in the structure of the kidney. In Tarsius only are the aortic vessels arranged in all examples as they are in Homo. The tongue of Tarsius shows the basal type to which that of Man may be referred. In most of those cranial features in which Man differs from monkeys, Tarsius resembles Man. Man resembles the monkeys in much. In more he resembles the anthropoid apes ; but in other points (which are not human specialisations) in which he differs from the anthropoid apes he still finds a likeness in this curious little creature. Tarsius we have assumed to be a very near likeness of Anaptomorphus of the Eocene—the first recognisable ancestor of the Anthropoidea. Man is undoubtedly linked to this early form by many bonds, and the bonds become less (except in purely superficial adaptive convergent likenesses) as advance is made *via* the inverted order of anthropoids and monkeys. In a very large number of features, Man, where he differs from the anthropoids, resembles Tarsius, and where the anthropoids differ from the monkeys they resemble Man. This distinction holds true in practically all cases, except

those which comprise what may be called definite human specialisations, those definite "progressive" features which distinguish Homo as a zoological type.

Such a finding places a topsy-turvy interpretation upon the end of the scale of life. Anaptomorphus of the Eocene and Tarsius of to-day, though specialised creatures, are in some respects the most primitive members of the Anthropoidea. Homo is specialised in his own definite directions, but is nevertheless next to this basal stock in order of general primitiveness. The anthropoid apes are specialised in their own different ways, but have an underlying primitiveness which links them to Homo. The monkeys both of the Old World and the New, while resembling the anthropoid apes in a general way, have departed in more respects from the basal Eocene type of the primitive ancestral form.

To the anatomist, Man must ever figure as a remarkably primitive Eutherian mammal. He is specialised from the basal stock in two main directions, (1) in the development of the brain, and (2) in the attainment of the upright position.

Probably no subject has proved more destructive of the reputations of anatomists than attempts at finding absolute distinctions between the brain of Man and the brains of the anthropoid apes. In the immediate post-Darwinian days the brain was regarded as the last hope of the older school, for surely, people argued, if we have to admit that the human body may prove upon dissection to be very like that of a chimpanzee, the human brain must show the utter and unfathomable distinction which separates Man from all the rest of the animal kingdom. And yet the champions of human cerebral distinctions fared very badly under criticism from the rising school. The disastrous argument about the hippocampus minor, which found its echo even in Charles Kingsley's *Water-Babies*, and in the pages of *Punch*, need not be recalled. The whole tedious literature which grew around the development of the "posterior lobe" leads to nowhere, and may be omitted. And yet, though all who sought to see anything but a simple evolution of the human brain from lemur, monkey and ape, came badly out of the argument, I believe that there

are few points in the whole of human anatomy upon which one could better defend the thesis that Man had evolved by no such simple route.

It has not been only the defenders of distinctions who have made their mistakes, and no such splendid fallacies as the theory of the "transitory" fissures can be laid at their door. But, though the ill-fated campaign of the hippocampus minor and the posterior lobe died a violent death amidst ridicule and loud-voiced triumph that all the world might hear, the "transitory fissures" were quietly laid to rest. No song of triumph was sung over their grave and even those who slew them turned silent from their last resting-place. And yet a great blow had been dealt in destroying for ever the far-reaching theories built upon such flimsy foundations. For the transitory fissures, which are present upon preserved human foetal brains of the third, fourth and fifth months, not being the forerunners of permanent human fissures, were said to represent cortical patterns of the lower animals, corresponding to the phase through which the human embryo, recapitulating its ancestral story, was passing. Here was demonstrable evidence of the stages through which Man had passed in his evolution—his whole phylogeny mirrored on his developing cerebral cortex. This was proof conclusive of the route by which Man had his origin. And now we know that these transitory fissures are mere artificial creases, due to shrinking of the thin, soft material of which the developing cerebral hemisphere is composed. As a withered apple puckers, so are the transitory fissures formed. This is material more fit for the columns of *Punch* than any deductions about the "hippopotamus minor." But the transitory fissures have slipped quietly away from us without a final gibe, without even an adequate obituary notice.

Man is an animal which has evolved, and which has taken his present dominant position, almost entirely by cerebral advance: of that there is no doubt whatever. But the question, Has this cerebral advance been made along the lines of the systematic arrangement of the order Primates? will, nowadays, receive a widely different set of answers. The most highly

developed structure is not necessarily the most highly specialised structure, for it is possible that the best may be produced by generalised development. Most will, I think, agree that therein lies the perfection of the human brain—it is a perfect example of generalised development of the Eutherian mammalian brain. It shows what may be called an all-round development. The brains of the anthropoid apes (and, with regard to perhaps the greatest number of isolated points, that of the gorilla) approach at times to a close approximation to this condition of human general development. But for the most part (and especially in the chimpanzee) they are committed to some side line of specialisation, which becomes more pronounced as the phylum of the Old World monkeys is passed in review. To take only one region of the brain, the chimpanzee appears to be definitely committed to that line of simian specialisation which finds one expression in the development of the so-called "simian sulcus," and I agree with those who see marked affinities to the baboons and macaques in the brain of the chimpanzee. The other anthropoids share definitely in this tendency, the gorilla inclining towards the lower African monkeys, the orang maybe more towards the Asiatic Semnopithecidae, but all towards the Old World monkey specialisation, not towards a primitive mammalian generalisation. The New World monkeys, on the other hand, appear to be not so definitely committed to those specialisations which are so characteristic of the Old World monkeys; and in the Woolly Monkeys (Lagothrix) there is evinced a tendency to generalised development which is strikingly reminiscent of human characters. So far there is but little recorded observation upon this subject, but nevertheless one may more aptly compare the mentality of the American monkeys with human cerebral processes, than we can grade over that very wide gulf which separates the mentality of the macaques and baboons from anything which is characteristically "human" in the best connotation of this word.

Even with such a slender outline as this it will be seen that there is some difficulty in imagining that human cerebral characteristics have been attained along the route of the

systematic arrangement of the Primates. That the underlying simplicity of the brain of Man can have passed from a stage, seen somewhat modified in the American monkeys, into the highly specialised stage of the Old World monkeys, and so again to the more generalised type of some of the anthropoid apes, is difficult to believe. That the brain of Man is the best expression of development of the brain of the Eutherian mammal is certain, and that it is an all-round development will be agreed by all. It is not a great step to admitting that the same story is unfolded here as elsewhere, and that the Old World monkeys and, in varying lesser degrees, the anthropoid apes show departures from this more generalised plan. That the brain of man might possibly be an evolution of such a primitive brain as existed at the base of the Primate stem; that the New World monkeys have not specialised far from this, but have undergone a somewhat even generalised development; that the anthropoid apes are comparatively little removed, and that the Old World monkeys have become most specialised off the line, appears to me to be a deduction drawn without undue straining of the facts.

Man's other great distinction—his upright posture—has accumulated such a mass of literature that an impression of hopelessness is left on the reader after a perusal of some of the hasty and bitter controversies that have raged around the question. That the "situs erectus" is not the prerogative of Man every one knows, and those who wish to underrate its human distinctiveness are welcome to all the comfort that may be derived from the study of the penguin. We may attach much, or little, importance to it, but nevertheless it remains as a very characteristic feature of Homo. There are those who regard human uprightness as being a very recently acquired readjustment from a previously pronograde quadrupedal habit. Man is regarded by many as having been fairly recently turned upright from a previous horizontal position. The whole summation of the anatomy of Man negatives any such conclusion. The human hand and forelimb tell a clear story, and in this story no chapter exists in which the precursors of Man walked the earth as four-footed

animals. Man, as I have elsewhere insisted,[1] came of an arboreal stock, his acquirement of the upright posture was initiated amongst the branches of the trees up which he climbed, and, as such, his uprightness is almost certainly an extremely old human possession. Arboreal uprightness and terrestrial uprightness are very different things, but Man has certainly converted the one into the other. Even terrestrial uprightness is no recent acquirement, as many would have us believe.

Blumenbach, and later Cuvier, were so impressed by the distinctions of the human foot that they conceived it only just to place its owner in a special order distinct from the monkeys and apes. This order they called Bimana, since with the specialisation of the foot Man became distinguished by the possession of two hands, and Cuvier defined hands as being members with one digit capable of opposition to the other digits. It seems almost incredible that Huxley should have argued that, since the American monkeys cannot oppose their thumbs, they cannot have four hands and so are ineligible for admission to the Quadrumana, but must be classed as Bimana, although their "hands" were situated upon their hind limbs. By such an argument was the order Bimana destroyed when destruction of human distinction was easy and popular. Even an attempt to emphasise the distinction of Man in possessing two feet fared no better. Huxley made short work of this claim. He showed how like the foot of Man was to that of the gorilla in the disposition of its bones, he pointed to the similarity of the muscles (but he failed altogether to note the beautiful difference in arrangement of the interossei muscles). But he was still faced by two facts that had to be argued away: the first that the big toe of the anthropoid apes is opposable, whereas that of Man is not, and the second, the remarkably different digital formula of the foot of Homo and the apes. In this dilemma he sought refuge, as so many have done, in the cramping effects of boot pressure. It is so easy to see in the habit of wearing boots the reason for the loss of the opposability of the human big

[1] *Arboreal Man* (Edward Arnold, 1916).

toe that it is rather pathetic to find Huxley falling back upon this argument. And it is surprising to find him instancing the mobility of the big toe of the unbooted savage as evidence of opposability. Every one is acquainted with the manifold uses to which the power of flexion, of adduction and of abduction of the big toe is put in unbooted races, but it is safe to affirm that no one has seen a native race in which opposability of the big toe exists. At the time, however, Huxley's tales of the Chinese boatmen, the Bengal weavers and the thieving Carajos satisfied his hearers and his readers that only a slight difference in degree separated the mobility of the human big toe from that of the ape; and another human distinction was swept from men's minds. As for the curious shape of the human foot, with its long big toe and the decreasing digital series to the almost rudimentary little toe, this was certainly very different from the outline of the ape's foot, but then what could be expected when toes were confined in boots?

This boot argument has proved such a talisman in accounting for the curious digital formula of the human foot that one despairs of ever seeing it eliminated from any discussion of the subject. Yet in truth it may be dismissed very simply. The peculiar, and absolutely specific, human digital formula is the same in the unbooted races as in the booted. In the baby at birth the big toe is just as dominant, and the little toe just as atrophic, as it is in the adult town-dweller who wears the latest dictates of fashion in the form of boots. More than this, the embryo within the uterus shows exactly the same features, and from that early time when digits first appear upon the limb-bud of the developing embryo the human foot is just as specific—just as distinct from anything seen in the monkeys or apes—as it is in the adult. This is a very simple and easily verified fact, but it is a very far-reaching one. Obviously if ontogeny recapitulates phylogeny the human foot cannot be a thing which, only slightly modified —and for the most part by boot pressure—departed from the type prevalent in the anthropoid apes by trivial readjustments acquired in very recent times.

It cannot be, as Huxley lulled his followers into believing,

that the human foot differs but little from the foot of the gorilla, and that such trivial differences as there are were acquired, as one might say, the day before yesterday. If any reliance at all is to be placed upon the order of ontogeny as an interpretation of phylogeny, then the very peculiar type of foot which is distinctive of Man has been a very early acquirement. We have already noted the very early differentiation of the peroneus tertius muscle, a muscle which is definitely associated with the human method of standing upright on the feet, and which is found in Man alone among the mammals. The early appearance of this muscle we may correlate with the early differentiation of the human type of foot. From a consideration of these facts we may logically argue that the habit of standing upright upon this foot is a very old, and not a very recent, habit.

We have therefore arrived, with the setting forth of only a very small portion of the material at hand, at certain definite conclusions. The first is that Homo is not descended from anthropoid apes preceded by a series of Primate forms represented by Old World monkeys, New World monkeys and lemurs. For we have seen that the anatomical characters of Man demand rather a recognition of the finding that his stock branched off from the very root of the Primates; that Tarsius is to be regarded as a specialised survival of the basal stock of the (non-lemurine) Primates; that Man has evolved entirely by generalised development of the brain, and that he retains the bodily simplicity only found in some such far-distant progenitor as the Tarsius stock; that, no matter what may be the relation of the New World and Old World monkeys, the human race combines, in some instances, a blend of their characters; that the anthropoid apes retain a certain, and a varying, amount of the basal simplicity that belongs to Man, but that the Old World monkeys have specialised far away from this simplicity. Regarded in this way we may say that the line of Homo springs from the base of the (non-lemurine) Primate stem and not from its systematic apex. And this conclusion, which is supported by a host of facts and contradicted by none, is

in no way surprising when one regards the findings of biologists and zoologists in their examination of phylogenies in other parts of the scale of life. But nevertheless such a finding is a serious one. Not only does it entail the belief that the origin of the human race is to be sought at the base and not at the apex of the Primate series, but it entails the belief that Man has, after his apprenticeship of arboreal uprightness, stood upright upon his specialised feet for a very long period of history. Such a belief would necessitate our imagining that in a very remote past ancestral Man became a more or less distinct creature which might be termed zoologically a "ground-ape"—a phase which the gorilla (already too far gone in simian specialisation) in part assumes to-day.

But from such speculations we are suddenly recalled to reality, for such speculations obviously permit an inference that an animal one might term semi-human might possibly be an extremely ancient animal—that a "missing link" might be, as Hubrecht indeed pictured it, an extremely ancient, small ground-ape not far removed from Tarsius, and no slouching product, half chimpanzee and half Man, of comparatively recent evolution. From that belief of Hubrecht I find it difficult to withhold sympathy. Man retains so many traces of mammalian simplicity, his body is so compounded of the most primitive mammalian features, that it is difficult to picture him as anything other than an extremely primitive mammal committed to a line of evolution which consisted almost entirely in the general and overwhelming development of the brain. So many of the primitive features which astonish us in Man are not possessed by the anthropoid apes that it is difficult to believe that Man could have arisen from any type at all similar to those living to-day; and as for the Old World monkeys, they are so definitely specialised in their own direction that they can in no wise be regarded as ancestral forms of Homo.

Having arrived at such a conclusion it remains to inquire if any known facts support the idea that Man, as a distinct zoological type, might have the astonishing antiquity demanded by such a picture of his phylogeny.

Concerning every find of the remains of Man which are of any considerable antiquity it is notorious that a preliminary warfare, conducted upon remarkably uniform lines, has been waged between two opposite schools. The one school, determined upon the recent origin of Man, has ever sought to discredit the find in some way or other, and the opposing school has laboured hard to establish both the humanity and the antiquity of the fragments brought to light. The Neanderthal type of humanity was branded as being no representative of any ancestor of Man, since it was undoubtedly pathological; it was the skull of a lunatic, it was the skull of a recently deceased Cossack — anything so long as it was not the skull of a normal, but very distinct, type of humanity contemporaneous with the geological evidences of its provenance.

We know now the universal, and undoubtedly well-founded, opinion regarding Neanderthal Man. Concerning the Piltdown individual there is still being fought the very same battle—obscured and passed over in consequence of the times in which we live—but nevertheless a battle just as keenly contested as that waged over other evidences of the antiquity of Man.

There is a school which regards Eoanthropus with perfect composure as a not very outlandish type of humanity, such as might be expected at the very base of the Pleistocene period; there are even some who, so to speak, would feel no shock at the discovery in the same Pleistocene bed of his silk hat and umbrella. On the other hand, there are some who, staggered at the undoubted antiquity of the remains, cannot bring themselves to picture the creature as other than grotesquely apish; even there is a strong school of those who, with a strange mixture of caution and temerity, regard the jaw of this type of humanity as being that of an actual ape, accidentally come into association with the skull of a real Man. For these last, though one can well appreciate the experiences that lead to their scientific caution, it is difficult to sympathise with their utterly unscientific credulity. It is just to strain at the gnat of the antiquity of Man as a zoological

type; it is another matter altogether to swallow the camel representing the belief that the skull of a unique type of humanity and the jaw of an ape, unique in its provenance, came into such close approximation upon the Downs of Sussex—the one having lost its own jaw, and the other its own skull, before their chance meeting.

But, whatever demands Eoanthropus may make upon our belief in the antiquity of Man, the Australian skull unearthed in 1884, but only properly described by Dr. S. A. Smith, of Sydney University, in the present year, increases our wonder, and leaves us gaping at the possibilities of future discoveries in the phylogeny of our species.

It is impossible to discuss more than the most simple facts concerning this evidence in the limits of so short a lecture; but within these limits the most salient features may be stated. This skull is highly mineralised, it is a "fossil" in the general acceptance of that particularly elastic word, it was washed by spate waters from a site 7 or 8 feet below the present earth-level at Talgai in the district of the Darling Downs of Southern Queensland. It is of little use to label it as "Pleistocene," since the extension of that term from Europe to Australia implies but little in actual geological sequence. Nevertheless far better evidence than that involved in a mere name is to hand. The skull is contemporaneous with extinct marsupials, such as the great Diprotodon and Thylacoleo; it is also contemporaneous with the fossilised teeth of a Eutherian animal—the dog. That the Eutherian dingo was a trespasser upon the Metatherian fauna of Australia every zoologist knows, but here is evidence that the trespass was made at a very remote period, and at this remote period the Eutherian dog also had as a contemporary another Eutherian mammal—Man. The supposition is that they trespassed in company; but think for a moment what this supposition implies. It means that these, almost the only Eutherian mammals which broke in upon the isolation of the Australian Metatherian population, came in the remote past, when many extinct Metatherians were flourishing, and that they alone were able to achieve the journey. No land bridge let them in, else a host of Eutherian followers would

have crossed " Wallace's line " in their company. Beyond a doubt they came by sea, and they came not as sea-tossed castaways such as are those animal pioneers that furnish the population of some distant islands. The progenitor of the Talgai Man came with his wife, he came with his dog and with his dog's wife, and he must have done the journey in a seaworthy boat capable of traversing this unquiet portion of the ocean with his considerable cargo. Besides this living freight, and the food and water necessary for the adventure, he carried other things—he carried a knowledge of the boomerang, of the basis of a totem system, and various other cultural features all bearing a strange suggestion of very distinctly Western origin. Beyond all this, and to increase our wonder, this man was already racially differentiated—he was an " Australian "—and he landed with his domesticated dogs in the Pleistocene of this New World almost the first Eutherian animal to break in upon a territory and a fauna not visited again by Eutherian mammals until the arrival of such as Captain Cook and La Perouse.[1] With such evidence to hand one may be quit of any haggling about the humanity of Eoanthropus, just as the knowledge of Eoanthropus relieves us of any care for the defence of Neanderthal Man.

That there have been many side branches of the Primate stock is not to be doubted ; that more ape-like types of humanity have sprung from the stem, as the apes themselves have done, is highly probable—even that the whole of the human race has not originated in one single point of departure is extremely likely. One fact we now know—that Man had domesticated the dog, had acquired some very highly specialised cultural distinctions, and was a complete navigator of oceans at a period of the world's history at which but a comparatively few years ago no scientific man would have admitted his existence as a zoological type.

With such a brief summary we must be contented in this

[1] The small rodents and the several species of bats which are found in Australia, though typical Eutherian animals, are here left out of account, since their facilities for dispersal are well known and their intrusion into the Metatherian fauna of Australia presents no problem.

hasty review of the problem; but it would be well to draw from this summary any lesson that may be applicable in the present time—and such is the purpose of this lecture. If we ask ourselves the question, Has humanity greatly benefited by the knowledge scattered broadcast throughout the world in 1859 ?, I think we must certainly answer that it has not.

This new creed fell upon the educated and the uneducated alike, it overwhelmed them all. For the comparatively few it taught the nobility of the recent achievement of Man's rise from brute creation; for all it inculcated a belief that his rise, noble though it might have been, was due to the natural selection of pure chance variations; for the masses it showed, by a transit marked by catch-words, a survival of the fittest by a crude struggle for existence from an extremely recent brute origin in the existing apes.

I believe that these doctrines have left their mark, that they are stamping present events with their impress.

Is there an alternative, is there a way out of believing that we are new-sprung from the ape by a process of chance variations leading to change of type after a pure brutish struggle for existence ? Were it not backed by demonstrated evidence it would be wrong—even in these times—to put forward such a view; but the evidence is to hand. It is upon the evidence that I have, in part, laid before you that I would urge you to reconsider the teaching of the immediate post-Darwinian school.

Man is no new-begot child of the ape, bred of a struggle for existence upon brutish lines—nor should the belief that such is his origin, oft dinned into his ears by scientists, influence his conduct. Were he to regard himself as an extremely ancient type, distinguished chiefly by the qualities of his mind, and to look upon the existing Primates as the failures of his line, as his misguided and brutish collaterals, rather than as his ancestors, I think it would be something gained for the ethical outlook of Homo—and also it would be consistent with present knowledge.

VI

SOME INHABITANTS OF MAN AND THEIR MIGRATIONS

By R. T. LEIPER, M.D., D.Sc.,
Reader in Helminthology in the University of London (London School of Tropical Medicine).

VI

SOME INHABITANTS OF MAN AND THEIR MIGRATIONS

FEW people care to confess more than a meagre and second-hand acquaintance with the parasitic worms which inhabit the human body. These slimy, loathsome and repellent creatures, with their subtle and apparently purposeless movements, their insidious and sustained effects upon the well-being of the living community of cells which harbours them, and their innate depravity, constitute in tropical lands at least a veritable "Enemy Within." It is an important part of the sanitarian's duties to keep them under surveillance and to checkmate their activities, for they are a constant menace to the public health.

Although insignificant in size, number and appearance, some of them are known to have exacted, from the earliest times, a heavy toll from human happiness and progress. Within the past few years, however, new knowledge, acquired not by the physician at the bedside but by the zoologist in the laboratory and in the field, has provided the means whereby the spread of these parasites can be definitely controlled. The chronic and often incurable diseases to which they give rise will eventually be eradicated.

"From a small text one can preach a large sermon and the proper sermon." One can find in the story of the migrations of this small group of animals alone ample evidence of the very real bearing which the study of animal life has on human progress.

Several of the worms which live in the human body and the

diseases which they cause were well known to the ancients. The Ebers Papyrus, written at Heliopolis about 1550 B.C., contains an account of a disease, UHA, caused by a worm, HELTU. This record is believed to refer to the "hookworm" or "ankylostome," which, at the present time, is the cause of a profound and intractable anaemia throughout the tropics, and which, in its economic importance, is second only to malaria.

Another of the diseases known to the ancient Egyptians and still very prevalent throughout Africa is one characterised by the passage of blood in the urine. On the walls of one of the temples in Egypt one may still see depicted the manner in which those about to bathe sought to protect themselves from the ingress of the parasite into the urinary passage. In one of the Pharaohs preserved in the Cairo Museum the late Sir Armand Ruffer detected, with the aid of the microscope, the minute, hard-shelled eggs of the "Bilharzia" parasites which are now known to be the cause of this bleeding.

The "Guinea-worm," which is common in West Africa and the Sudan, and is met with all over India, often in epidemic form, is referred to by Plutarch in his eighth book of *Table Talk*, written about 150 B.C., where he relates that "the people taken ill on the Red Sea suffered from many strange and unheard-of attacks, amongst others from little snakes which came out upon them, gnawed away their legs and arms, and when touched again retracted, coiling themselves up in the muscles and there giving rise to the most insupportable pains." An earlier reference to the same disease is seen by some in the account of the "serpents" which afflicted the Children of Israel in their wanderings from the Red Sea. For centuries the recognised mode of dealing with this snake-like worm, which is nearly a yard long, has been to wind it slowly out from the intensely burning or "fiery" ulcer which it causes, usually on the limbs, by coiling it round a piece of stick. The "pole," bearing the "fiery serpent,"[1] is thus believed to represent, in symbolic form, an eminently successful method of treatment, just as the "emerods" and the "golden mice"

[1] As seen in the familiar badge of the Royal Army Medical Corps.

which the Philistines returned with the Ark of the Covenant reveal still to the understanding mind the intimate association of rats with bubonic plague.

The Mosaic injunction against the use of certain animals as "unclean" was apparently rightly based upon the fact that these food-animals harbour "cystic" worms in their tissues, some of which, as we shall see shortly, have been proved to be the infective stages of tapeworms in man. Tapeworms were well known to Hippocrates, for he describes a case in which considerable lengths of worm were seen to leave the body. The animal nature of the "hydatids" or cystic worms was clearly suspected in the Middle Ages.

For long the peculiarly repulsive disease of the tropics called elephantiasis was confused with leprosy, but as early as A.D. 1037 Avicenna clearly distinguished the "Elephantiasis of the Arabs," which Sir Patrick Manson has shown to be associated with the presence in the lymphatics of a thread-like worm, from "Elephantiasis Graecorum," the true bacillary leprosy.

Thus the presence of living worms, often incapable of movement and in some of the most inaccessible organs of the body, has always been a source of interest and mystery to physicians and naturalists alike. Throughout the Middle Ages it was universally believed that they originated spontaneously within the body, and discussion was confined simply to the particular manner in which this "spontaneous generation" came about. By some it was maintained that the worms "arose" from ill-digested food in the alimentary canal or from the secretions of the digestive glands; others held that they originated from the blood and from "corrupt juices" in various organs of the body. It was much disputed whether the first impulse of creation was due to fermentation or putrefaction or to a special organising principle.

Even as late as 1853 we find the following opinion: "In the predisposition to worms the thick mucus of the intestine comes under our consideration. From a portion of the mucus the worms are produced by spontaneous generation with the assistance of Asthenia and Dynamia"!

These fantastic theories received their death-blow from the application of zoological methods and ideas about fifty years ago. The microscope revealed for the first time the fact that the parasitic worms produce enormous numbers of eggs. Obviously, if these millions of eggs could develop and attain their maturity in the intestine in which they were laid, the unhappy host which harboured them must perish with all his parasites. Necessarily, therefore, the eggs must be discharged to the outside. Consideration of the further fate of these eggs brought about a revolution in current views on the source of parasitic infections. It was seen that danger did not arise from within but, through contamination of the environment, from without. It was realised that the parasites of man were not a peculiar people of human origin but part of the fauna of the outside world, which had, for purposes of better food and shelter or for the propagation of their species, adapted themselves to a parasitic habitat within the human body during a phase of their life-cycle.

We know now that the sexually mature worms cannot reproduce a new generation of adults within their host. Each adult worm must have entered the body as a microscopic form. We know also that, with a possible single exception,[1] the eggs or young of these parasites cannot immediately infect another person after they have passed out of an infected person. A period of delay must first intervene before the young forms attain sufficient maturity to become "infective." The changes which take place in the young parasite during this period are such that the resulting "infective stage" has no likeness to the newly born. Similarly it bears no resemblance to the adult into which it will eventually develop.

As long as the infective stage could not be recognised the physician had no means by which he could prevent the spread of the disease except by destroying the parasites through the administration of drugs to all infected persons; by securing the control and safe disposition of all human excrement, and by enforcing the sterilisation of all food and drink not collected from sources free from the possibility of contamination.

[1] *Oxyuris vermicularis*, the "seat" worm common in children.

Such procedure would involve vast expenditure, ceaseless educational propaganda and constant co-operation of all members of the community. Yet, without a knowledge of the conditions governing the life of these parasites outside the body, it would prove of no avail against many of the infections met with in tropical countries.

Against certain of the parasitic worms drugs are impotent. The disposal of human excrement would not necessarily break the "cycle" of many infections, for zoologists have found that the domesticated animals often harbour the same species of parasites as those found in man, and thus act as "reservoir" hosts, and, again, while some species are undoubtedly taken into the human body in food and drink, some of the most important forms have recently been shown to enter through the skin by their own activity. Moreover, although the progeny of many of the parasitic worms leave the human body in the stools, there are some which pass out in the sputum and the urine, while others are sucked from the blood by biting insects.

One can best meet danger if one knows whence it must come. By divers zoological methods the naturalist has enabled the sanitarian to recognise with certainty the "infective stage" of each of the species which cause disease in man. He has been able to show that each parasite has its own special method of approach and that this practically never varies. It has, in consequence, been possible to devise a simple and efficacious control over the ingress of each species.

In another and still more far-reaching way the naturalist has come to the aid of the sanitarian. We have seen that the physician can only rid his patient of certain of his parasites, to wit, some of those which live in the alimentary canal. Those which inhabit the liver, lungs, glands and blood-vessels are inaccessible to the action of drugs. Moreover, the administration of "anthelminthics" is not without danger, as these are poisons and can therefore only be given in minute doses. During the "period of delay," in which the parasites undergo development outside the body, they are much more susceptible to attack. The naturalist has studied in detail the various

stages of this development and the exact conditions under which it takes place. It has been found that parasites cannot proceed in their predestined course, and necessarily die, unless certain very special circumstances prevail.

In some species these factors in success are matters of temperature, humidity etc. In other species the young worm must obtain, within a brief period, shelter and nutriment in some particular invertebrate or even vertebrate host, in which to undergo its essential metamorphosis. Where this is the case the naturalist has been able to indicate means whereby the particular essential intermediary may be eradicated and thus the life-cycle of the parasite be inevitably broken. In fact, it is not too much to say that the elimination of this special class of diseases will eventually depend upon a scientific application of zoological data derived from the study of the migrations, outside the human body, of the parasites concerned.

I now proceed to summarise various discoveries that have been made during recent years regarding the migrations of the more important parasites of man, and to show how in each case the facts obtained have already proved of inestimable value.

One of the earliest and most important observations was that made by Kuchenmeister on the nature of the bladder-worms which are found in organs of the body unconnected by natural passages with the outside. These parasites never develop genitalia nor give rise to eggs, and it was difficult to explain how, otherwise than by "spontaneous generation," they came to be present in the tissues or how they could reproduce. For a time it was thought that they were merely tapeworms which had strayed from their normal habitat in the intestine and had become degenerate and dropsical in consequence of their unusual environment. This hypothesis was apparently strengthened by the discovery that at one spot in each cyst there was always a bud bearing four suckers, which greatly resembled the head of a normal tapeworm. In 1851 it occurred to Kuchenmeister to test the matter by

feeding an animal with some of these cysts. A cyst, taken from the brain of a sheep suffering from staggers, was given to a dog; shortly afterwards the animal was found to be suffering from tapeworms and numerous tapeworm eggs were observed passing in its excrement. Some of these eggs were then fed to sheep. The animals soon showed symptoms of "staggers," due to the pressure of growing cysts on the surface of the brain.

This successful experiment led Naunyn to feed a dog with one of the large cysts, called "hydatids," which at times produce serious and even fatal disease in man. Numerous minute but sexually mature tapeworms resulted, which proved to be identical with those found in a dog in 1809 by Rudolphi and then believed by him to have arisen by spontaneous generation from the villi lining the intestinal wall.

Meanwhile Kuchenmeister had continued his observations. Having noted that a marked similarity existed between the hooks borne by the bud in the cystic worms found in pork and those on the head of the common tapeworm found in man, he administered a number of these cysts to volunteers. Later he found that he had successfully infected them with the hooked tapeworm, *Taenia solium*, thus implicating the pig as the vehicle of the infective stage. Pigs were then fed with eggs from the excrement of a person infected with *Taenia solium*. When killed later the flesh was found to be infested with typical cysts.

As no adult tapeworm was found to occur in the intestine of the pig it was evident that the development of the "dropsical" or "cystic" stage was a normal and not merely an aberrant phase in the cycle of the *Taenia solium*.

For years it had been observed that among the hooked tapeworms of man specimens sometimes occurred from which the hooks were entirely absent. The generally accepted explanation was that these were old and decrepit individuals which had lost their hooks, just as with advancing years the teeth and hair fall out in man. Leuckart, however, having heard that this type of tapeworm was common among the natives of Abyssinia—who do not keep pigs but rear cattle in

large numbers—determined to feed a calf with eggs passed by a patient known to be infected by this hookless form. The calf, when killed later, was found to be infested with cystic worms which had a somewhat different appearance from that of the cystic stage of the armed tapeworm from the muscles of the pig. Some of the cysts were swallowed by a volunteer in whom they developed into tapeworms of the *hookless* variety. These experiments, which apparently proved that man harbours, in his alimentary canal, not one but at least two species of tapeworm, developing respectively in the pig and in cattle, were at first received with incredulity, for cystic worms had never been recorded in cattle killed at the abattoirs. When specially looked for, however, they proved to be of quite common occurrence.

These studies in experimental zoology revealed the source of the " infective " stage of three of the important tapeworms of man and led to the routine meat inspections by our public health authorities, which are now so efficiently carried out that tapeworm infection is relatively rare in this country. They showed too that certain parasitic worms at least require a second and different species of host in which to pass a portion of the life-cycle and that each species has its own special intermediary. Thus, the armed tapeworm can only attain its cystic infective stage in the pig, while the hookless form can similarly develop only in cattle.

The importance of experimentally determining the special intermediary host for each species is illustrated by the migrations of the " broad " tapeworm,[1] which is a common parasite in man in the countries bordering the Baltic and in Switzerland. This species is practically unknown save where fresh-water fish form an important item of diet. In 1881 Braun found in the flesh of perch, pike and allied fish a larval stage which when swallowed by volunteers eventually developed into mature specimens of the " broad " tapeworm. Fresh-water fish, then, were undoubtedly the essential intermediaries of the " infective " stage. Repeated experiments, however, failed to produce the developmental stages by submitting

[1] *Bothriocephalus latus*, sometimes termed the Irish tapeworm.

these species of fish to infection with the eggs of the adult parasite. Last year, however, Janicki showed that a second intermediary is essential. After hatching from the eggs, the tapeworm young are pursued and swallowed by a species of Cyclops. In the body of this minute crustacean—the so-called "water-flea"—they undergo a preliminary development. If the infected Cyclops is swallowed by a perch, for example, the parasite is set free and migrates into the muscles of the fish and there, after further growth, attains the infective stage; remaining in this situation until the fish is in turn eaten by a human being.

Nearly related to the tapeworms are the flukes or Trematoda. Perhaps the best-known example of the group is the liver-fluke, *Fasciola hepatica*, which infests sheep and cattle and causes heavy losses in all meat-producing countries. In man, allied species of flukes inhabit the liver, the lungs and the blood-vessels, especially in tropical lands, where they cause grave and incurable diseases. There is no successful method of attacking the adult flukes and there seems little probability that they will be eradicated by drug administration, as they reside in situations inaccessible to medication. As in the case of the tapeworms, however, zoological studies have enabled us to attack these parasites successfully during their migrations outside the body.

Our knowledge of these migrations dates from a remarkable series of observations made by the Danish zoologist van Steenstrup. Several groups of "asexual flukes" had been recognised by early workers in invertebrate zoology. These had been placed in isolated "genera," to which the names Redia, Cercaria etc., were given. Thus the so-called genus Cercaria comprised larval Trematoda which enjoy the power of free locomotion in water and are provided with a tail wherewith to propel themselves. It was recognised that this form was not a permanent one, but the changes which it underwent were unknown. Steenstrup showed that these free-swimming "cercariae" in some instances attacked

fresh-water snails and in the tissues of these became "pupae." Within these cysts there were found later young forms which were to all intents immature flukes.

Having, on morphological grounds, linked the free-swimming cercaria with the fluke, he then proceeded to trace the connecting link between the cercaria and the egg. To the question, Whence comes the free-swimming cercaria? he found an answer already at hand in an observation made by Bojanus, who had described cercariae swarming out from "king's yellow worms," which occur in great numbers in the interior of snails and which possess the characters of the so-called genus to which the name Redia had been given. These rediae or cylindrical worms of Bojanus resemble in structure neither the flukes into which their progeny eventually develop nor the young larvae which hatch out of the fluke eggs. It was evident then that another stage of development must intervene. Steenstrup found this link in some observations published several years previously by Siebold. In most flukes the larva only develops within the egg after this has been laid, but in a fluke called *Monostomum mutabile*, which frequents the cranial cavities of certain water-birds, the eggs develop while still within the parent. Siebold had remarked that in this species the ciliated larva, developing within the egg, always harboured another and totally dissimilar body which he called the "necessary parasite." Steenstrup recognised that this so-called parasite bore an undeniable resemblance to the "rediae" or worms of Bojanus, and thus finally linked together "redia" and "cercaria" as different phases of one life-cycle.

In zoology, at any rate as applied to medicine, the inductive method has its special perils, but of Steenstrup's remarkable deductions it may be truly said that "Observation is blind unless the eye is informed by knowledge. It is observation 'loaded with inference' that alone gives insight."

The knowledge that the flukes require a molluscan intermediary host in which to undergo their extraordinary metamorphosis, and that thereafter they may encyst in a second intermediary before gaining their final or definitive host,

remained for many years a matter of purely zoological interest. Steenstrup had published his researches in 1842. At that time the fluke parasites of man had not been discovered. In 1853 Bilharz found adult flukes (now known as Bilharzia worms) in the portal veins of a patient who had died of Egyptian haematuria. The Asiatic liver-fluke, *Clonorchis sinensis*, was first seen by McConnell in the bile-ducts of a Chinaman who died in Calcutta in 1874, and in 1880 Sir Patrick Manson forwarded to Cobbold the first specimens of the lung-fluke, *Paragonimus ringeri*, found in a native of Formosa.

During the succeeding years information gradually accumulated which showed that each of these flukes frequently gave rise to widespread and incurable disease in the regions in which it was endemic. The need for preventive measures became more and more appreciated and the physician once more turned to the naturalist for guidance.

The questions calling for solution were not those which concerned the mode of development of the flukes outside the body, for the work of Steenstrup and others had definitely shown that the flukes during their free stage parasitised and multiplied within some species of mollusc. The special information required was (*a*) what was the exact means used by the "infective stage," *i.e.* the cercaria, of each species to enter the human body ? and (*b*) was there any phase in the development of the parasite outside the body in which it was specially susceptible and could be easily and cheaply destroyed ?

For the three chief types of flukes which invade man satisfactory answers to these questions have been forthcoming. It remains only for the sanitarian to put into effective use the scientific data available.

The lung-fluke and liver-fluke of man are confined almost entirely to the Far East. It has been proved that these and a third species, which, though a common intestinal parasite, causes no symptoms in man, require for their larval development a special fresh-water snail of the genus Melania, viz. *Melania libertina*. After metamorphosis the "cercaria" in each case becomes free-swimming and then attacks a second

host, in which it remains encysted until this vehicle-host is eaten by man as food. For each species, however, the second host, *i.e.* that in which the cercaria or "infective stage" encysts, is not the same. The lung-fluke, after passing through Melania, utilises certain fresh-water crabs as a means whereby to reach man in encysted form. The two other flukes encyst in a variety of fresh-water fishes which have this in common—that they are usually consumed as human food.

Taking the zoological facts concerning these three flukes together, two methods of prevention obviously present themselves. Either the use of fresh-water crabs and fish must be restricted and these animals only allowed as food after sterilisation by heat etc., or some attempt must be made to eradicate the molluscan intermediary which is essential to the development of all three parasites. The latter plan seems the simpler and the more feasible. In Korea some preliminary experiments have already been undertaken to determine whether, by the collection of Melania, its local incidence can be kept under control.

The Bilharzia worms [1] live in the blood-vessels and give rise to eggs which, after migrating through the tissues, erode their way through the walls of the bladder and gut, causing symptoms of haematuria and dysentery. The eggs of these flukes are passed in the urine and excrement. It has recently been shown that they hatch in water and give rise to ciliated bodies which attack certain species of fresh-water snails. The metamorphosis which then takes place follows along lines similar to those characteristic of flukes generally, and the final stage leaves the snail as a free-swimming form. This cercarial or "infective" stage, however, does not encyst in some food-animal, as described above for the other fluke parasites of man. It has been proved, by experiments upon rats, guinea-pigs and monkeys, that in the case of the Bilharzia worms the free-swimming cercaria can actively force its way into the human body through the skin and that a second intermediary or vehicle-host is therefore unnecessary.

[1] There are three species, viz. *Schistosoma haematobium, Schistosoma mansoni* and *Schistosoma japonicum.*

These experiments support irrefutably the common but vaguely held view that infection occurs in many instances during bathing. It had been shown that the young, newly hatched larva is killed by acid of the dilution of 1 in 1000, and from this it was concluded that infection by the mouth could not take place owing to the lethal action of the gastric juice. A study of the free-swimming cercariae showed, however, that these attach themselves firmly to the lining of the mouth when given in drinking-water to monkeys, and that these animals later succumb to intense infections of Bilharzia worms. Infected water is therefore dangerous whether used for drinking or for ablution.

The measures which have been outlined above for the control of fluke diseases in the Far East are obviously inapplicable to bilharziasis. The collection of the molluscan intermediaries would be attended with grave risk owing to the ease with which the parasites can penetrate the moist skin. In a country like Egypt, where bilharziasis is so prevalent, it would be impracticable owing to the enormous numbers of irrigation channels and drains, in which the snails find ideal breeding-places. The sterilisation by heat of all water for drinking and ablution would likewise be impracticable. Sedimentation and mechanical filtration through sand at first sight offers a promising method of dealing with large quantities of water, especially in view of its undoubted success in mechanically detaining bacteria. Unfortunately the free-swimming infective stage of Bilharzia actively maintains itself near the surface of the water. It is not entangled in the scum which successfully retains bacteria on the surface of a sand-filter, for by its vigorous movements it not only quickly pierces this but can migrate through the sand without inconvenience. Preventive measures have therefore once more to be based upon a study of the bionomics of the parasite and of its intermediary host.

After the cercaria has left its molluscan host it does not feed again until it has entered its definitive host—man. During its stay in the water it is constantly moving and thus rapidly exhausts its initial energy. It has been found that

the duration of life of the cercaria as a free-swimming organism does not exceed forty-eight hours. If, then, water containing the infective stage of Bilharzia is simply stored for about two days it becomes free from infection.

A study of the fresh-water snails now known to spread the disease in Egypt has revealed certain biological facts which, if properly used, may result in a marked diminution if not in the eradication of bilharziasis over a wide area. Unlike the Melania and Katayama snails which spread disease in the Far East, the Bilharzia carriers in Egypt are not provided with an operculum by means of which they can close their shells and so withstand drying for a long period. Exposure and the Egyptian sun ensure their death in a few days.

In Egypt these carriers of Bilharzia live and breed chiefly in the irrigation channels, the water running in which is entirely under the control of the Irrigation Department throughout the country. In the summer months the flow is carefully regulated and the water is periodically cut off entirely for some days. During such stoppages the snails which carry the Bilharzia die off, in enormous numbers, from drying. Unfortunately the beds of the irrigation channels are often uneven from the removal of mud for brickmaking etc., and pools result. In these residual patches of water large numbers of the Bilharzia-carriers congregate and so survive until the flow of water is again established. I am convinced that, without interfering with the general scheme, the summer rotations might easily be utilised, with slight adjustments, to bring about the complete eradication of the Bilharzia intermediaries. Where the alignment of the canal cannot be readily altered the pools could be effectively dealt with by chemical means. Certain of the common chemical manures are highly toxic to these fresh-water molluscs, and yet no possible harm could result to the crops from their use.

During the summer months there is absolutely no rainfall in Egypt, and the existence of the Bilharzia-carriers is dependent entirely upon "controlled" water. It is therefore surely incumbent upon the Irrigation Department in Egypt

to do something to assist in the eradication of this disease, especially as there are good grounds for believing that its incidence has become much more intense since the introduction of perennial irrigation.

In other lands, where the snails live in natural water-courses and the climatic conditions are less constant, the problem of Bilharzia-prevention becomes more difficult and necessarily more dependent on personal prophylaxis.

We pass now to the roundworms or Nematoda, which form by far the greater proportion of the Entozoa of man. The various species present very different modes of migration but space does not permit of details. In some cases, as in the common roundworms met with in this country, development takes place within the egg-shell, which, after a necessary period of delay, again enters the body as an accidental contamination of food.

The Trichina worm develops in the pig. The infective stage is encysted in the muscles, but is usually destroyed by our British custom of cooking pork until it is white. In Germany, where pig-flesh is used as raw food, trichinosis is common.

In the case of the Filaria worms, which cause diseases of the lymphatics and are responsible for the onset of elephantiasis, the young worms, circulating in the blood, are sucked up by a mosquito and undergo development in the tissues of this insect, returning again from the mosquito to another human host.

Many of the roundworms, after hatching from the egg, spend their entire "period of delay" as free-living forms, finding sufficient nutriment in the organic matter in the soil, where they undergo their metamorphosis and remain quiescent until taken again into the body.

The manner in which the migrations of the Guinea-worm and the Hookworm were elucidated call for special notice.

The adult Guinea-worm (*Dracunculus medinensis*) is a parasite which lives wholly in the connective tissues under the

skin. When sexually mature it discharges a very powerful irritant which causes the overlying skin to ulcerate. Through the ulcer the worm slightly protrudes and discharges a milky fluid. Under the microscope this fluid is seen to contain myriads of active young. These young can live in water for about a week, but they do not grow or feed and eventually die.

In the intestine of the perch, in the upper reaches of the Thames and in nearly all continental rivers, there lives a peculiar, blood-sucking roundworm, *Cucullanus elegans*, which has no morphological resemblances to the Guinea-worm. The young of these two worms are, however, extraordinarily alike, and differ from the young of other parasitic forms in several remarkable features.

Comparing these larvae Leuckart arrived at the conclusion that their peculiar structure is a special larval adaptation to assist them in attacking some special intermediary. He succeeded in showing that Cucullanus larvae invade the bodies of small crustaceans of the genus Cyclops and in them undergo a complete metamorphosis, and he maintained that the similarly formed larvae of the Guinea-worm would be found to follow the same course. At his request the Russian traveller Fedschenko undertook to test the hypothesis while visiting Persia. The results of the experiments completely substantiated Leuckart's views. The young Guinea-worms entered and metamorphosed in the bodies of Cyclops. Some years ago I was able, in West Africa, to show that, after completing this metamorphosis, the larvae become quiescent and remain encysted in the body-cavity. When monkeys were fed with these infected Cyclops, the larvae, released by the gastric juice, made their way into the connective tissues, where they were found after several months to have developed into almost full-grown Guinea-worms.

These facts concerning the life-history of the parasite provided a simple and efficacious method of avoiding this disease in infested countries. Water has only to be strained through a pocket-handkerchief to be freed from any Cyclops which it contains and which might harbour the infective stage of the Guinea-worm.

In heavily infected countries the disease appears to be contracted chiefly from isolated and much-used ponds, or from wells. Probably a further study of the bionomics of the parasite and of its intermediary will show that only certain species of Cyclops act as efficient hosts and that small collections of water can be freed from these small but dangerous crustaceans.

There is romance even in the lives of worms. I close with the life-story of the ankylostome worms (*Ankylostoma duodenale* and *Necator americanus*), the remarkable wanderings of which were first revealed by a laboratory accident.

The "ankylostome" or "hookworm" is an intestinal roundworm about half an inch in length, which infests over 50 per cent of the inhabitants of tropical and subtropical countries. In Porto Rico, at one period, it was responsible, directly or indirectly, for 30 per cent of the annual mortality. Even as a mild infection it is the source of much invalidity and heavy economic loss. The "laziness" and general degeneracy of the "poor white trash," who are said to belong to the purest-blooded English stock in the United States, are due not so much to environment and heredity as to the ravages of these parasites.

In a public lecture, delivered before the University of Pennsylvania in 1915, Allen J. Smith, citing the factors which have caused the Southern States to lag in American progress, maintained that hookworm disease "stands with malaria as worse than war and the devastation of battles and worse than all the other pathogenic agencies in combination." Through the influence of these diseases "the men and women of the South, bred from the best American colonial stock, offspring of pioneers, with the blood of English gentry and continental cavaliers in their veins, sank lower and lower in physical degeneration and squalor; were derided and denounced as lazy and shiftless and condemned in popular opinion as worthless and a disgrace."

The hookworm is one of those roundworms which do not require an intermediary host. The eggs hatch and meta-

morphosis takes place in moist soil. Many years ago Leuckart traced this extra-corporeal phase in a closely allied species which infests dogs, and found that the infective stage is taken into the body in drinking-water.

In 1894 Looss, while studying the metamorphosis of the worm as it occurs in man in Egypt, accidentally let a drop of water, containing the developing worms, fall upon the back of his hand. Some minutes later an intense itching sensation developed at the same spot. Seeking an explanation for this annoyance he concluded that it must have been due to something in the water which had been wiped off—either to some irritant or toxic substance secreted by the growing worms or to invasion of the skin by these microscopic forms. A part of the same culture was then filtered and the clear water was applied to another portion of the skin. No irritation followed. The young worms, in fresh water, were then applied and again intense irritation was set up.

From these experiments Looss concluded that the ankylostome worm is able to enter the human body through the skin. Some weeks later additional evidence was forthcoming, for symptoms of hookworm infection began to manifest themselves and the eggs of the hookworm were passed in numbers in the excrement.

With metamorphosed larvae of an allied species, *Ankylostoma caninum*, a natural parasite of the dog, Looss then carried out an exhaustive series of experiments which conclusively proved that, after piercing the skin, the larvae enter the small veins and are carried to the heart. Thence they pass in the blood-stream to the lungs. In the lungs they are eventually stopped in the fine capillaries, through which they are too large to pass. The larvae then burst into the air-sacs, whence they are carried by the mucus into the bronchioles. They are found later in the trachea, and, being swallowed, pass into the gut, where they finally attain their full maturity.

This entirely novel route was at first received with scepticism but was quickly confirmed by other workers. In England, and in America, volunteers submitted to experimental infection. Successful and indeed severe infections

followed the careful application of hookworm larvae to the skin.

Looss' researches, the outcome of a laboratory accident in the course of a purely zoological investigation, profoundly altered our conceptions regarding the mode of spread and prevention of hookworm disease. Protection of water-supply could only play a small and insignificant part in prophylactic measures against a parasite which was likely to enter the body whenever the skin came into contact with a moist contaminated surface, for statistical studies showed that cutaneous infection was actually responsible for over 90 per cent of the cases investigated.

In the parasitic infections hitherto considered it has proved possible to rely for preventive measures on an attack upon the special intermediary or the vehicle-host. In the case of the hookworm, not only is an intermediary host absent, but the terminal phase of development, *i.e.* the "infective" stage, forms by ecdysis a peculiarly resistant skin in which the larva can survive for many months without food and with a minimum amount of moisture. Moreover, these are spread over enormous areas.

Under these circumstances the attack has had to be transferred to the eggs before they are disseminated and to the adult worms. In other words, eradication of this disease depends upon the efficient disposal of night-soil and upon the destruction of the adult parasites living within the body.

Fortunately the ankylostome is an intestinal worm and is peculiarly susceptible to certain drugs. By treating infected persons, not only are these individuals relieved of their parasites but they cease to be a source of danger to others.

There was little hope that ankylostome infection could be stamped out by such measures as these so long as the cost and responsibility of carrying them out depended upon the initiative of infected individuals. Persons harbouring only a few worms would feel no ill-effects and would therefore be unlikely to pay for treatment. Nevertheless these persons would continually pass living eggs in their excrement and thus be a menace to others.

It is not too much to say that, in 1909, a new chapter opened in the history of disease-prevention when the interest of Mr. John D. Rockefeller was successfully enlisted in the problem of hookworm control. The Rockefeller Sanitary Commission, during the succeeding five years, found that "more than two million people in the Southern States were infected with hookworm, involving vast suffering, partial arrest of physical, mental, and moral growth, great loss of life, and noticeable decrease in economic efficiency over vast regions." The Commission also ascertained from extensive inquiries that in the inhabited territory between thirty degrees north and south of the equator more than a thousand million people harbour the parasite; that infection in some nations rises to nearly 90 per cent of the entire population; that this disease has probably been an important factor in retarding the economic, social, intellectual and moral progress of mankind, and that even where it is most severe little or nothing is being done towards its arrest or prevention.

In 1913 Mr. Rockefeller endowed the International Health Board with one hundred million dollars "to extend to other countries and peoples the work of eradicating hookworm disease," and to establish agencies for the promotion of public sanitation and the spread of scientific medicine.

By December 1915 nearly one and a half million people had been examined, and of these 593,383 were subsequently treated. During 1916 specially organised campaigns were in progress in the Southern States of America, in the West Indies, in British and Dutch Guiana, in Egypt and in Ceylon. The methods followed so successfully enlisted the confidence and co-operation of the people that the vast majority voluntarily submitted to examination and treatment. In British Guiana 94·4 per cent of the population within the region of operations were examined; of these, 62·3 per cent were found to be infected and 84·3 per cent of the infected were cured. In St. Vincent 99·9 per cent of the people within the area submitted to examination and 84·9 per cent of the infected were cured. A beginning only has been made in this beneficent work.

VII

THE FUTURE OF THE SCIENCE OF BREEDING

By R. C. PUNNETT, M.A., F.R.S.
Arthur Balfour Professor of Genetics in the University of Cambridge.

VII

THE FUTURE OF THE SCIENCE OF BREEDING

To speak upon a subject prescribed by authority is never an easy matter, and when the subject implies a knowledge of the future it is apt to give one pause. For prophecy, as we all know, cometh not by the will of man. But in my hesitation I recalled that most eloquent chapter of Butler's in which are set forth the views of the Erewhonians upon the future—how the future is already in the loins of the past, and how we can but guess at what is coming by the tenor of that which we have seen. If, therefore, I speak of the past it is of the past in its anticipation of the future. And this I can the more readily do because our past is so short that it is almost entirely to the future that it belongs.

Since the present century opened no advance in knowledge among the biological sciences has been so momentous as that which has taken place in the province of heredity and variation. Indeed the change of outlook has been so marked as to bring about the use of a new term—genetics—for studies which lie along these lines. The science of genetics concerns itself with the phenomena whereby one generation of plant or animal is linked with the generation preceding it and with the generation which follows—with that which it begets and with that by which it was begotten. It strives after the understanding of that hitherto mysterious process whereby germ cell springs from individual, and individual in turn arises from germ cell.

It is common knowledge that our first real insight into this process was due to Gregor Mendel. His masterly experiments with peas led him to a conclusion which was as novel as it was

far-reaching. It had been proved before Mendel's time that the genesis of a fresh individual commenced with the fusion of two germ cells, one from the male and one from the female parent. The identities of these two germ cells, or gametes as we now call them, were regarded as entirely merged in the identity of the resulting individual, or zygote, which henceforth possessed a unit identity of its own. Mendel's discovery has led us to regard the zygote as a compound or dual structure, of which the exhibited characters are dependent sometimes solely upon the one or the other of the two gametes of which it is compounded. The process by which gametes arise from the zygote is a process by which the duality of the zygote is resolved as it were into its components, and the gametes so produced are again units capable of uniting with others to form dual structures once more.

If all the gametes are precisely alike, zygotes resulting from their various fusions will also be all alike and we shall be dealing with a uniform strain. A true-breeding race of Black Rosecomb Bantams forms such a strain, and the White Rosecombs form another. A pure black Rosecomb was formed from two black gametes, and the dual structure which it represents was formed of like components (Fig. 1). When, therefore, the dual structure is resolved and gametes arise from it these are all alike,[1] *i.e.* all black. So also the gametes of the White Rosecombs are all white. Now what happens when White and Black Rosecombs are mated together? Experiment has shown that the offspring are all black. The influence of the black is dominant. Nevertheless we know from the form of the experiment that our dual structure here is formed from unlike components, viz. one "black" gamete and one "white" one. What is going to happen when such a dual structure is resolved—when it itself gives rise to gametes? The answer to this question has been deduced from the results of breeding such birds together (Fig. 2), and of crossing them back with the parental strains (Fig. 3). When mated together they give blacks and whites in the ratio of 3:1; when crossed

[1] Excluding, of course, those differences upon which the manifestation of sex depends.

back with the whites they give equal numbers of whites and blacks. Moreover, the whites which appear, whether from the mating between two blacks or from the mating between black and white, never throw blacks again but behave like the whites of the pure white strain. The inference from these facts can

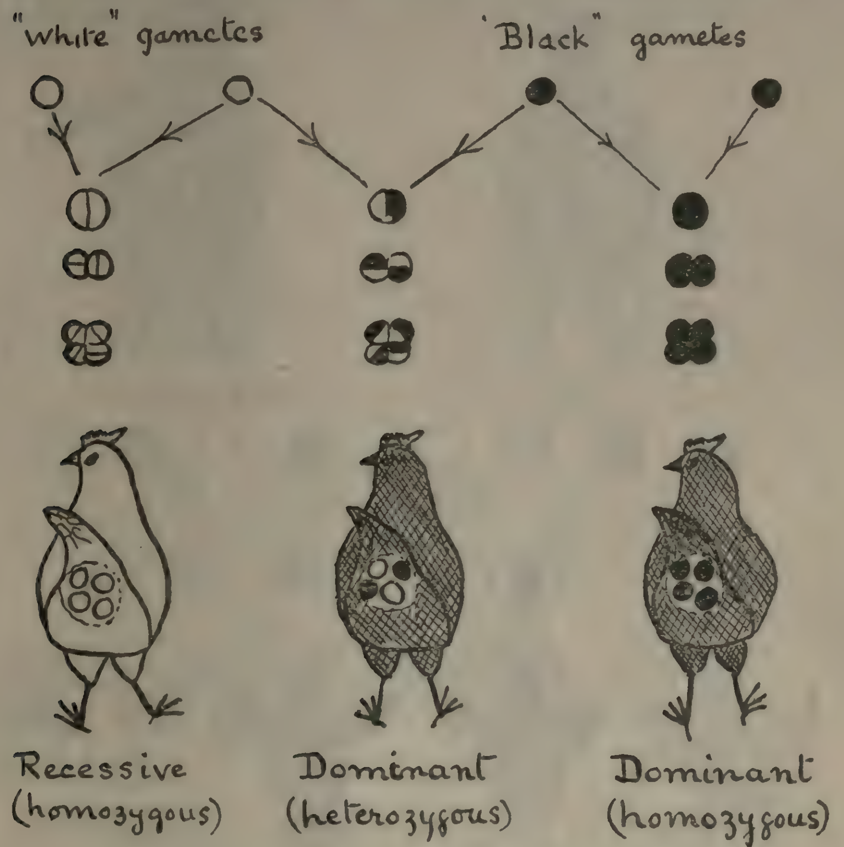

FIG. 1.—Diagram showing the three types of zygotic combination which it is possible to produce from the two sorts of gametes, white and black. The black and white circles shown inside each bird represent the nature of its output of gametes.

only be that the first-cross birds form two kinds of gametes, and two only. Further, the numerical proportions given above force us to conclude that the two kinds of gametes are formed in equal numbers. In other words, when the duality of the hybrid zygote is resolved, half of the resulting gametes are like those peculiar to one of the original parental strains, and half are like those peculiar to the other.

This is what is meant by "purity of the gametes," a conception which is the very essence of Mendel's discovery. But, one may ask, the purity of the gametes for what? In the case of the Rosecombs it stands for something which makes

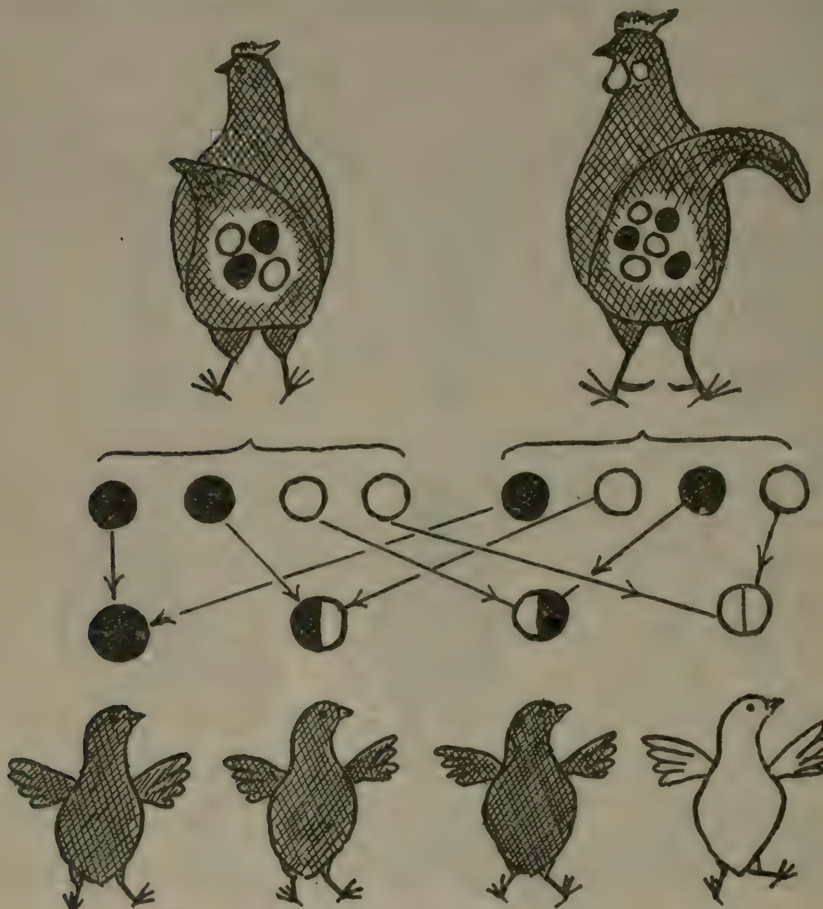

FIG. 2.—Diagram showing the result of mating together two heterozygous birds. Each produces an equal number of "black" and of "white" gametes, and the result of bringing together two such series of gametes is a generation of chicks in which the blacks are three times as numerous as the whites. As indicated in the figure, the blacks are constitutionally of two sorts. The true-breeding blacks, viz. those formed by the union of two "black" gametes, form one third of the total blacks produced.

the difference between black plumage and white plumage. We may suppose that the gametes of the blacks possess a something, possibly of the nature of an enzyme, or the precursor of an enzyme, which brings about the change, while the gametes

of the whites are without it. For this something, whatever it may be, we use the term factor, and it is with respect to these factors that we term the gamete "pure." Whether these factors are really permanent and indivisible without losing their distinctive properties, in the sense that chemical molecules are permanent and indivisible, or whether they can

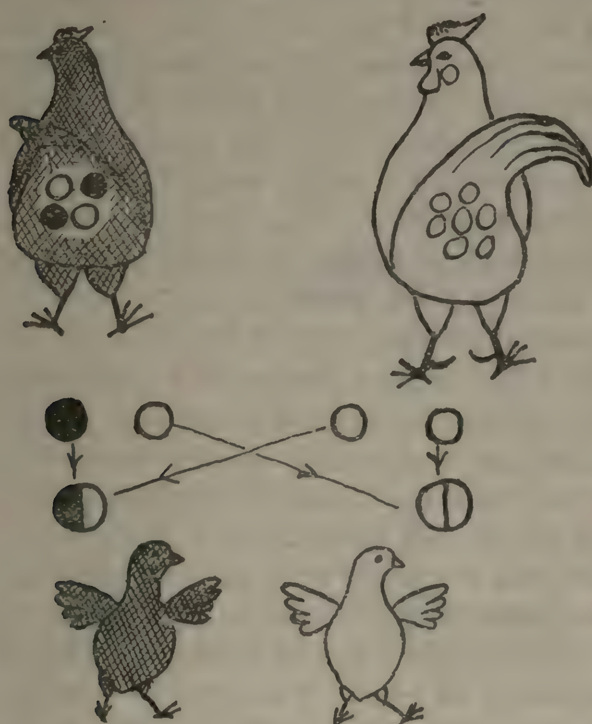

Fig. 3.—Diagram showing the result of mating a heterozygous black with the recessive white. Equal numbers of black and white chicks are produced, and all of the blacks are heterozygous.

be fractionated, is a question on which, at present, there is a difference of opinion, as we shall see later. For the moment we will assume that they are definite indivisible entities.

We spoke of the first-cross Rosecombs as forming only gametes of the two parental types, and in this particular case it is true. But every breeder knows that when first-cross animals are bred together, however pure the parental strains may have been, the progeny are usually exceedingly diverse.

This "breaking of the type," as the breeder terms it, is, for him, one of the most familiar of phenomena. How are we to reconcile it with the conception of gametic purity? Perhaps a simple case may serve as an illustration.

Let us suppose that our original cross is between two strains which differ in the form of the comb as well as in the colour of the plumage, and that our cross is between a black rosecombed bird and a white bird with a single comb. If certain strains of these are used the offspring are black rosecombed birds. When bred together they produce four kinds of offspring, viz. black rosecombs, white rosecombs, black singles and white singles, and the proportion in which these four forms appear is approximately 9 : 3 : 3 : 1. Two new forms have appeared—white roses and black singles, or, as the breeder might prefer to put it, the types with which we started have been broken. The explanation becomes clear if we regard it, not from the standpoint of the original parents as a whole, but from that of the two contrasting pairs of characters, black and white plumage, rose and single comb, which went into the cross. In the first cross black is dominant as before, while in the next generation blacks and whites are as 3 : 1. So also rose is dominant in the first cross, while the next generation consists of roses and singles in the ratio 3 : 1. Any given gamete arising from the first-cross birds is pure for the property of transmitting either black or white. At the same time it is pure as regards the property of transmitting either rose or single comb. But the plumage factor and the comb factor are independent of one another. Though the first cross has been formed by the union of a black rose with a white single gamete, the gametes that arise from it consist of black singles and white roses, as well as of the two parental types. And the breeding results force us to conclude that these four kinds of gamete are produced by such birds in equal numbers. An orderly redistribution of the factors takes place somewhere in the cell divisions which lead up to the formation of gametes in the cross-bred. Though the original parental types are broken and fresh types appear in the second generation, this in no wise militates against the conception of the purity of the gametes. And

this is confirmed by the fact that the new types can at once be fixed and made into true-breeding strains.

The illustration just given is of purpose a simple one, but it is clear that if the original parents differ in a larger number of factors the diversity of the second generation will be correspondingly greater. The recognition of this principle of the orderly assortment of factors among the gametes has rendered possible that detailed analysis of plants and animals which has made such rapid strides during the past few years. Analysis of this kind aims at the determination of every factor in a species by which one individual may differ from another. Mendel himself determined seven such factors in the pea. The number has now grown to thirty-five and includes such characters as flower-colour, seed-shape, height, pod-structure, foliage-form and flowering period. Many factors have also been definitely determined in the cereals and in other plants, though in no case is the analysis approaching completion. Since upon it depends the breeder's estimate of the possibilities of making new and improved strains, as well as the facility with which he is able to attain his end, it is natural that attention in many quarters should be more directly focussed upon plants of economic value. Owing to the heavier expenses connected with their breeding, animals have not been analysed to the same extent. There is, however, one valuable exception, the little pomace fly (Drosophila), in which Professor Morgan and his collaborators claim to have determined over one hundred different factors. To this small and important creature we shall have to return later.

Now all this work is merely an elaboration of Mendel's original communication. The method was laid down by him, and the theoretical conceptions upon which the method was based were clearly stated in his masterly essay. Though the work is of to-day we are dealing with the scientific past. Nevertheless the geneticist is not yet brought to a standstill. There is for him a scientific present full of novel conceptions which are being put vigorously to the test. A keen spirit of controversy animates the genetic world—always a healthy sign. I may perhaps dwell briefly upon a few of these

questions of the present, for out of them some day must come the progress of the future.

Linkage.—One of the earliest departures from the then recognised scheme of Mendelian inheritance was found in what is often termed linkage of characters. The cases are peculiar in that the orderly distribution of the factors among the gametes is disturbed in an orderly manner. Purple flower colour, for example, is dominant to red in the sweet pea. The sweet pea is also noteworthy in that some plants produce three-pored oval or long pollen while others have round pollen with

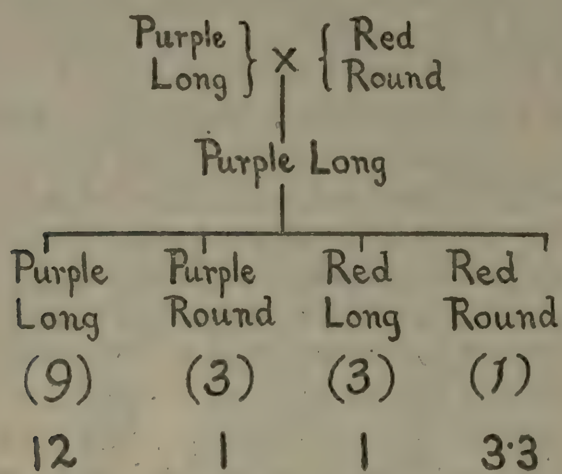

FIG. 4.—For explanation see text. The numbers in parentheses indicate the proportion of the four forms which would be expected if the case were one of simple Mendelian nature. The line of figures below gives the actual proportions of the four forms as found by experiment.

two pores. Of these, long is dominant to round. When a purple long is crossed with a red round (Fig. 4), the offspring are all purple longs. Were the case one of simple Mendelian heredity the offspring of such plants should be of the four types—purple longs, purple rounds, red longs and red rounds, in the ratio 9 : 3 : 3 : 1. As a matter of fact the four expected classes appear. Further, the ratio of purples to reds is 3 : 1, as also that of the longs to rounds. The peculiar feature of the case lies in the distribution of the four classes taken together. The purple longs are about twelve times as numerous as the purple rounds, while on the other hand the red longs are barely

more than one-quarter of the red rounds. In other words, the factors for purple and for long are linked together so that the two classes of gamete, purple long and red round, are about seven times as numerous as the two classes purple round and red long. Without this complication the four classes of gamete would of course have been produced in equal numbers. It will be noticed that the two types of gamete which preponderate among those formed on the first-cross plant are the two original parental types—the new combinations purple round and red long being in the minority. Now make the

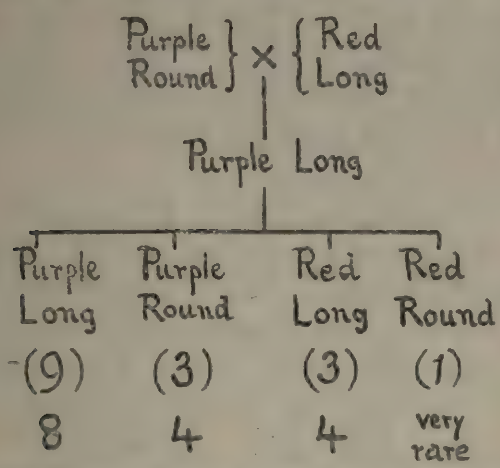

FIG. 5.—For explanation see text. The numbers in parentheses indicate the proportion of the four forms which would be expected if the case were one of simple Mendelian nature. The line of figures below gives the actual proportions of the four forms as found by experiment.

cross the other way about, crossing a red long with a purple round (Fig. 5). The hybrids, or F_1 plants, are purple longs, indistinguishable in appearance from the purple longs which arise from the union of a purple long and a red round gamete; nevertheless these purple longs when bred from give an entirely different kind of family. The four types are all present, but the purple longs are about twice as numerous as the red longs or the purple rounds, while the red rounds are extremely rare, less than $\frac{1}{2}$ per cent of the total. This result can be explained on the assumption that the purple round and the red long gametes arising from the first-cross plants are about seven times as numerous as the purple long and the red round

gametes. Again you will notice it is the two parental combinations which preponderate. The combinations which go into the cross together tend to come out together.

Since it was first discovered in the case of the sweet peas, this phenomenon of linkage of factors has been observed in other plants and also in animals. The more thorough the analysis the more frequently does this phenomenon appear. More than two factors may enter into one of these linkage systems. In the sweet pea, for example, the factor which causes the standard to become erect instead of hooded shows linkage relations with the factors for long pollen and purple flower-colour. In any cross involving all three of these factors the general rule holds good. Those which go in together into the cross tend to come out together, though the linkage is never absolute.

Through the energy of Professor Morgan and his colleagues the study of this phenomenon has recently led to developments of unusual interest. The American workers here had the advantage of using extraordinarily favourable material in the pomace fly (Drosophila), and it is not too much to say that this little creature is to the geneticist what the frog has long been to the physiologist. Besides the rapidity with which it can be bred and the large numbers produced by a single pair, it presents a very considerable number of characters which have been proved to follow the ordinary scheme of Mendelian heredity. We have already seen that the American observers claim to have identified over a hundred factors, affecting most of the external characters. As was to be expected in a form in which the analysis has been pushed so far, linkage phenomena have been encountered in abundance.

A remarkable feature of the case is that the analysed factors fall into four groups. All the members of a given group show linkage with one another but not with the members of the remaining three groups. Now it is significant that in Drosophila there are four pairs of chromosomes. This at once suggests that each of the four groups of factors is related to a given pair of chromosomes. Moreover, there are two further facts which strengthen the suggestion of such a relation. In

the first place, one of the groups of factors is very small, containing only two factors, as compared with the 20-40 of the other groups, while one of the pairs of chromosomes is also very much smaller than the others. Secondly, there are grounds for supposing that one pair of chromosomes is definitely connected with sex determination, and at the same time it has been demonstrated that one of the groups of factors is peculiarly related to sex, whereas the other three groups are independent.

A strong *prima facie* case is thus made out for the close connection between chromosomes and factors. But here a difficulty has to be faced. If two factors belonging to a given group, let us say those for grey colour as opposed to black and for long wing as opposed to short, both enter by the same gamete—it matters not whether by the maternal or the paternal one—then we should expect these factors to keep together when a series of gametes arises. If gametogenesis implies merely the resolution of the dual structure of the cells of the individual, merely the separation of the descendants of the maternal and paternal chromosomes which went into the cross between long-winged grey and short-winged black, then the only two kinds of gamete should be grey long and black short. As a matter of fact it has been shown experimentally that a certain proportion of grey short and black long gametes are also formed.

The American school gets over this difficulty in a most ingenious way. Some years ago it was shown by the cytologist Jannsens, that at certain stages in cell division the chromosomes of some animals tend to coil round one another, spiralwise. It is suggested that at the points of closest contact the paired chromosomes stick together, so that when the subsequent separation occurs portions of the paternal and maternal members of the pair become interchanged (Fig. 6). In this way is formed a certain proportion of chromosomes in which the factors for grey and long wing have become distributed by "crossing over" as it is termed. These are the chromosomes which enter the gametes that give rise to the short-winged greys and the long-winged blacks respectively.

If this process occurs and if the factors are arranged in a linear series along the chromosomes it is clear that the nearer

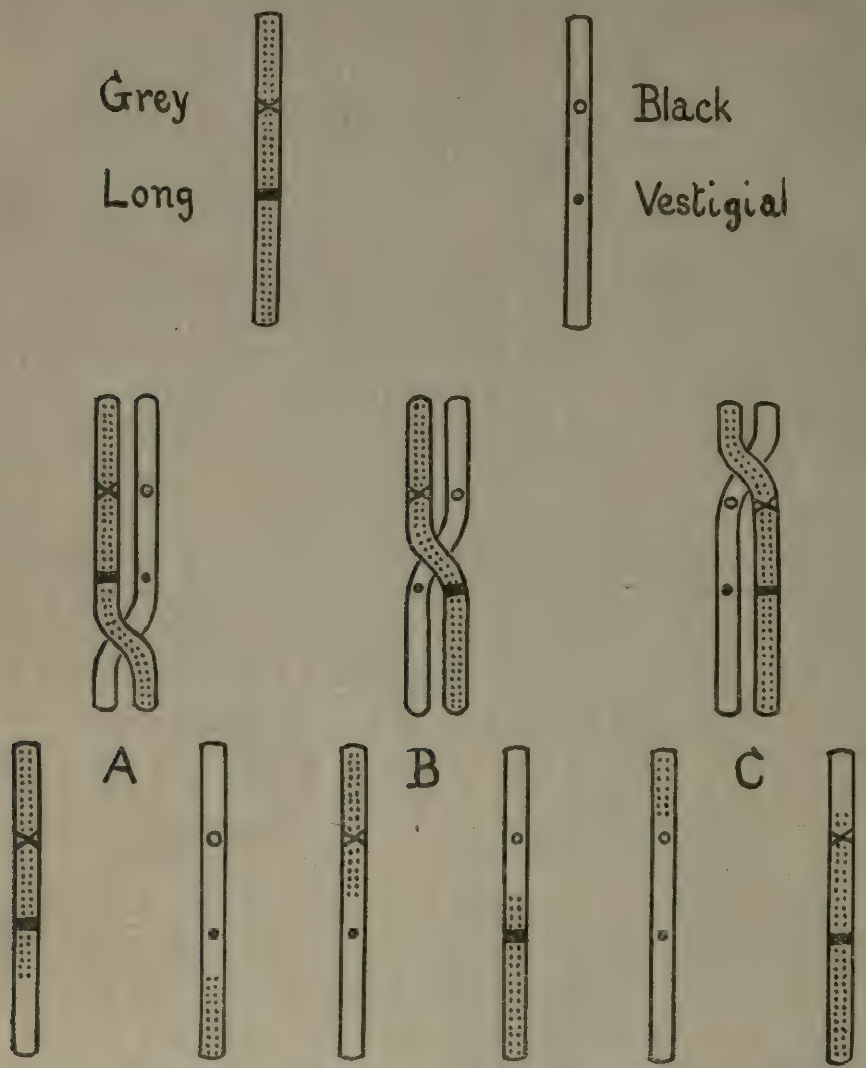

FIG. 6.—Diagram illustrating the conception of "crossing over" among the chromosomes, as developed by the American school. Whether crossing over of the factors for "grey" and "long," and for "black" and "vestigial," occurs, depends upon whether the point of junction and subsequent breaking between the chromosomes falls in the area separating the factors, or beyond it on either side. Crossing over of the factors in question occurs in B, but not in A or C.

they are together the less the chance of their becoming separated. On the basis of these assumptions and of the observed value of the intensity of linkage between the various

factors belonging to a given group, the American workers have mapped each of the four chromosomes of Drosophila as regards the position of the different factors, and the fact that the results are on the whole self-consistent is further evidence in support of their hypothesis.

There are some difficulties in the way of this interpretation, but to discuss them is beyond the scope of this essay. Nevertheless all biologists must feel that the work constitutes a great step in advance. Many a barren discussion has taken place as to the physical basis of heredity. Now at last, through the application of genetic methods, we appear to be getting some insight into the matter, and the suggested correlation between the facts of breeding and cytological phenomena offers fair hopes of substantial progress in the near future. The physicist has been able to demonstrate the molecule ; it may be that the biologist will soon be able to demonstrate the factor, that penultimate entity upon which so many of the phenomena of life depend.

Sex.—A line of genetic inquiry which has attracted many workers is that of the experimental analysis of sex. The fact that the two sexes are, among the higher animals, generally produced in approximately equal numbers, at once suggests that one of the sexes is recessive and the other heterozygous for a factor upon which the distinction between male and female depends. But which of the two was to be regarded as containing the factor lacking in the other was a question insoluble without further data. Fortunately such data soon became available in the form of those peculiar cases called sex-linked.

Many breeds of poultry possess both gold and silver varieties, which, as a rule, differ only in the ground colour of the plumage being golden orange or white. Gold and silver pencilled Hamburghs are a good instance, while the little gold and silver laced Sebright bantams are another. Experiments have shown that silver behaves as a dominant to gold, but there is a remarkable peculiarity in the results obtained from reciprocal crosses (Fig. 7). When a silver cock from a pure silver strain is crossed with a gold hen, all the chickens

are silvers. But from the reciprocal mating of gold cock and silver hen the male offspring are all silver and the females all gold.

Extensive analysis of this and of other cases of similar nature in poultry has led to the conclusion that the female is the heterozygous sex. No silver hen, however bred, has yet been found to be homozygous for the silver factor. Nor, when mated with a gold cock, has such a hen ever been known to give a silver daughter. We are led to suppose, therefore, that she produces two kinds of eggs, viz. those

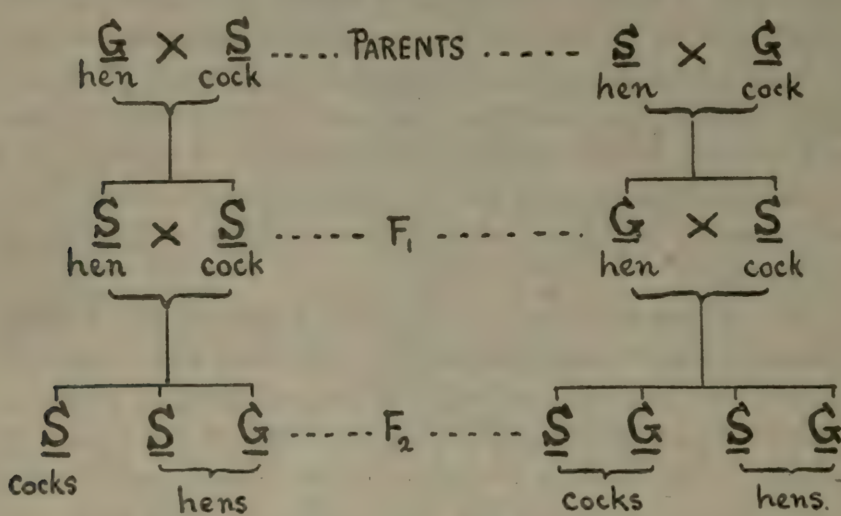

FIG. 7.—Scheme illustrating the different results obtained in the reciprocal crosses between gold and silver fowls. For further explanation see text.

which carry the silver factor but not the factor for femaleness, and those which contain the female factor but not the factor for silver. The fact that she can be proved to be always heterozygous for silver, which we know to be dominant to gold, and the further fact that she can transmit this factor only to her sons, force us to conclude that she is also heterozygous for the factor which decides whether a chicken is to be a hen. Experimental work has also shown that other birds, such as pigeons and canaries, resemble poultry in this respect, as also does the common currant moth.

Sex is apparently such a deeply seated feature that we

might have expected other animals to fall into line with this conception of the nature of the difference between male and female. Curiously enough, however, this is not so. Soon after the discovery and elucidation of sex-linked phenomena in the bird and in the moth a case of peculiar interest was found in the pomace fly (Drosophila). Normally the eye is red, but in certain cultures a few white-eyed individuals appeared. These turned out to be males, and experiments showed that white eye is recessive to red. Mated with red-eyed females the white-eyed males gave only red-eyed offspring. Subsequently white-eyed females were obtained, and it was found that these, when mated with any red-eyed male, gave red-eyed females and white-eyed males only. As in the poultry, the reciprocal crosses produced an unlike result. But, whereas in the fowls it is the female with the dominant character that is always heterozygous, in Drosophila it is the male. Hence we must infer that here it is the male that is heterozygous for a sex-factor.

Since the case of the white eye was worked out, the same type of sex-linked inheritance has been demonstrated for a number of other characters in Drosophila, and a careful study of these has led Professor Morgan and his collaborators to the conclusion that they are all contained in the same member of the four chromosomes which are present in this species. For not only do these characters exhibit sex-linked inheritance, but they also show, in the female, that peculiar form of linkage among themselves which we have already described.

But what is the form taken by the sex-factor itself? The Drosophila workers consider that the determination of sex is a function of a whole chromosome, viz. the chromosome in which the sex-linked factors reside. From recent cytological work it appears that there is a visible difference in the sexes in respect of one of the chromosome pairs. In the female the two members of the pair are indistinguishable, but in the male one is like those found in the female, while the other presents a slight but definite difference in that one end is bent over in the form of a hook. It is to this pair of chromosomes that sex-determination is attributed. The straight

chromosome is known as the X chromosome, and the bent one is termed the Y chromosome. Normally, then, every female has two X chromosomes, while every male has one X and one Y chromosome. Or, to state it in another way, every fly which receives an X chromosome from each parent is a female, while the fly that receives an X chromosome from its mother and a Y chromosome from its father is a male.

Striking confirmation of this explanation has recently been brought forward by Bridges. As the result of abnormal cell divisions flies are occasionally produced which receive two X chromosomes from their mother and a Y chromosome from their father. Nevertheless the presence of the two X maternal chromosomes decides their sexual fate. They are females in spite of the male Y element. Other observations of the highest interest in this connection have been made by Bridges, to whose paper must be referred those who are interested in these matters. For us here the outstanding feature of it all is that a definite and not unsuccessful attempt has been made to link up hereditary characters with definite and visible structures in the cells of which animals and plants are composed.

If this line of work ultimately makes good it may bring within the bounds of possibility the alteration of the hereditary properties of germ cells by direct action through physical or chemical means. The biologist of to-day inclines to the view that new characters in plants or animals are generally initiated in the cell divisions which give rise to the germ cells. Were the normal distribution of hereditary stuff at such divisions disturbed, we should obtain new combinations, some of which might very well be stable. If it be proved that the chromosomes are the bearers of this hereditary stuff we are clearly in a better position to appreciate the most favourable moment to bring extraneous influences to bear. I have little doubt that attempts will soon be made to bring about fresh groupings of the chromosomes, whether by magnetic, electrical or other means, and I am quite prepared to hear of such attempts being attended with success.

Secondary Sexual Characters.—Sex itself is, after all, but a

portion of the problem of sex. Equally arresting in the scheme of things are those characters which, normally the property of one sex, are upon occasion appropriated by the other. The hind may sprout antlers, the cock may become broody or the woman may grow a beard. The study of these secondary sexual characters, characters not directly concerned with the primary function of reproduction, is becoming a subject of genetic inquiry. We cannot yet claim that great progress has been made, but the following example may serve to indicate the lines along which such inquiries are being directed.

In certain breeds of poultry the plumage of the cock resembles that of the hen. He is destitute of the long, silky and often brightly coloured feathers on the neck and back which are generally associated with this sex, nor has he the usual curved, flowing sickles in the tail. Breeding experiments have proved that "henny" feathering in the cock is dominant to normal cock feathering. The "henny" cock contains some factor which prevents the development of the normal cock plumage. What of the hen? Is her plumage "henny" because she also contains this factor? And in normal breeds do we get "cocky" cocks and "henny" hens because this factor is somehow sex-linked and transmitted to the hens alone?

That this is a reasonable way of looking at the matter is evident from the remarkable experiments of Goodale and of Morgan in America. Those of Goodale deal with the effects of castration in a breed of fowls, the brown Leghorn, in which the sexes differ markedly from one another in plumage. In the male the operation produces practically no effect; the feathering after moulting is as before. But removal of the ovary from the hen, an exceedingly difficult operation, led to a marked and surprising result. Such a bird may moult into the full cock plumage, though the general habit of her body remains that of a hen. The castration story agrees with the conception of the hen being potentially cock-plumaged but unable to show it owing to the possession of a factor which inhibits the development of such plumage. And it adds something further; for we must suppose that the

functional activity of this inhibition is dependent upon the integrity of the genital gland. Remove the ovary and the inhibition no longer works. The castrated hen dresses like a cock.

What then is this inhibition? Were it not for the existence of henny cocks we might be tempted to ascribe the effect to the direct action of the ovary itself. But the existence of these birds clearly puts such a simple explanation out of court, for it is certain that they do not possess an ovary. At this stage Morgan's experiments come into the story. He has castrated a number of these henny cocks and has arrived at the curious and paradoxical result that the removal of the male genital gland leads to the assumption of the complete male plumage. In the henny cock as in the hen herself the activity of the inhibitor is dependent upon the integrity of the genital gland. But the inhibition itself is a definite thing, transmitted on Mendelian lines, and only dependent upon the sexual gland in so far as it requires some secretion from either ovary or testis to call it into activity.

From experimental work of this sort the nature of secondary sexual characters is assuming a new aspect. Qualities which we have hitherto regarded as the perquisite of one sex may nevertheless occur and be perpetuated in the other. For analysis suggests that they are not merely the expression of a particular form of sexual gland, but are, in many cases at any rate, based upon independent hereditary factors, and therefore subject to independent transmission. Whether there will be any economic outcome from all this, for my own part I feel little interest to inquire. After all, we are men and women before we are breeders of animals and plants. It is the evaluation of our own sexual properties, the determination of our own potentialities and limitations, that we are coming to discern in the study of these secondary sexual characters. They must ever remain the warp upon which is woven the woof of our own social life. It is for us to try so to understand our material, its peculiar weaknesses and strength, that upon the warp allotted to us we may weave our fabric at once both splendid and enduring.

Quantitative Cases.—Many of the characters with which the breeder deals are of the sharp, clean-cut order. The alternative characters are easily distinguished. A flower is purple or it is red, a bantam is white or it is black, an animal is male or it is female. The difference is a qualitative one and readily appreciated. These are cases of the simplest kind, but, as every breeder knows well, a cross between two pure strains may give a great number and confusion of forms when carried to the F_2 generation. Take for example the case of the sweet pea. If we make a cross between the salmon-orange "Barbara" and a lavender such as "R. F. Felton," the resulting plants are a reddish mauve and quite unlike either parent. In the next generation a considerable range of colours and shades appear. Some are like the original parents, some like the first cross, and many new forms turn up of which some can be recognised as varieties already standardised and named.

With a little care and a few years' work we can sift out and fix these many forms. What appeared at first sight a compound mass of blending colours can be analysed into a number of separate and distinct components. In spite of the appearance of grading and blending the differences are all qualitative. Such a case as this of the sweet pea offers no special problem or difficulty for the ordinary methods of Mendelian analysis.

There are, however, large groups of results which cannot as yet be expressed clearly in terms of qualitative factors. They are to be met with more especially where such characters as size, weight, extent of pigmentation and so forth are concerned. To put it crudely, the problem with which they challenge us is a quantitative rather than a qualitative one. Size inheritance *may* be straightforward. Many cases are known where a dwarf plant behaves as a simple recessive to a tall one. In all such cases it will probably be found that the dwarf is not merely a tall with all its parts reduced to scale. It will differ in habit as well as in bulk. The factor on which the size difference here depends is fundamentally a qualitative one.

But there are other cases in which the study of the inheritance of size brings to light a more complex result. In illus-

tration I choose some experiments with poultry carried out by the late Major P. G. Bailey and myself. We crossed the Sebright bantam with one of the smaller full-sized breeds, the gold-pencilled Hamburgh. Roughly speaking, the Hamburgh is about double the weight of the Sebright. The first-cross

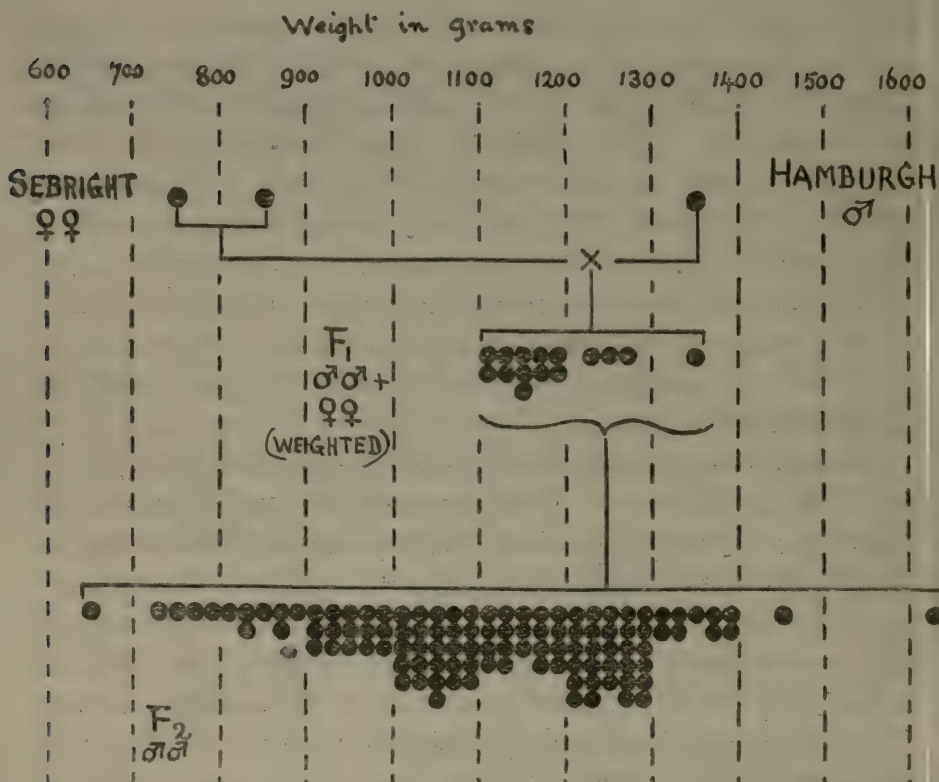

FIG. 8.—Diagram showing the experimental results obtained by crossing silver Sebright bantams with a gold-pencilled Hamburgh cock. Since in poultry the hen is always lighter than the cock, the F_1 hens have been "weighted," *i.e.* multiplied by a constant factor (found experimentally), to bring their weights up to those of the corresponding cocks. In the F_2 generation the records of the cocks only are shown. A similar result was obtained for the hens.

birds were intermediate in size, though they approximated more closely to the larger Hamburgh (Fig. 8). Bred together they gave rise to an F_2 generation ranging from birds smaller than the Sebright to birds larger than the Hamburgh, the majority, as the curve shows, being intermediates of various weights.

This indeed is the general experience of those who have studied crosses involving quantitative characters, whether in animals or plants. The first crosses are more or less intermediate in size between the parental breeds, while at the same time their range of variability is relatively small. When they are bred together they give rise to an F_2 generation in which the mean, as in the F_1 individuals, is roughly intermediate between those of the original strains used. The great difference between the F_1 and F_2 generations is that, whereas in the former the range of variation is comparatively small, in the latter it is very large, overlapping and sometimes even exceeding the range found in the two parental strains. The salient feature about such an F_2 generation is that the curve of variation is apparently continuous. Even the closest scrutiny will not enable us to separate them into definite groups, as was possible with our sweet peas.

How are we to bring such cases into line with those in which the phenomena can be explained in terms of definite factors each producing a definite qualitative result? A form of explanation favoured by many genetic workers is that recently termed the theory of multiple factors, of which the conception was originally due to Nilsson-Ehle. On this theory a cross may involve a difference between the original parents of several factors, each independently producing a similar effect and each transmitted in the normal way.

Perhaps the simplest way of making this clear is to take a simple imaginary example (Fig. 9). Let us suppose that a cross is made between two animals of which one is homozygous for three independent factors A, A^1 and A^2, the other lacking in all three. Let us also make the following assumptions :—

(1) That each factor by itself produces a similar effect in increasing the size.

(2) That a double dose of any of the three factors produces twice as great an effect as that resulting from a single dose.

(3) That the independent effects produced by the three factors are cumulative.

Then the original cross means the union of a gamete (AA^1A^2) containing all three factors with one (aa^1a^2) that

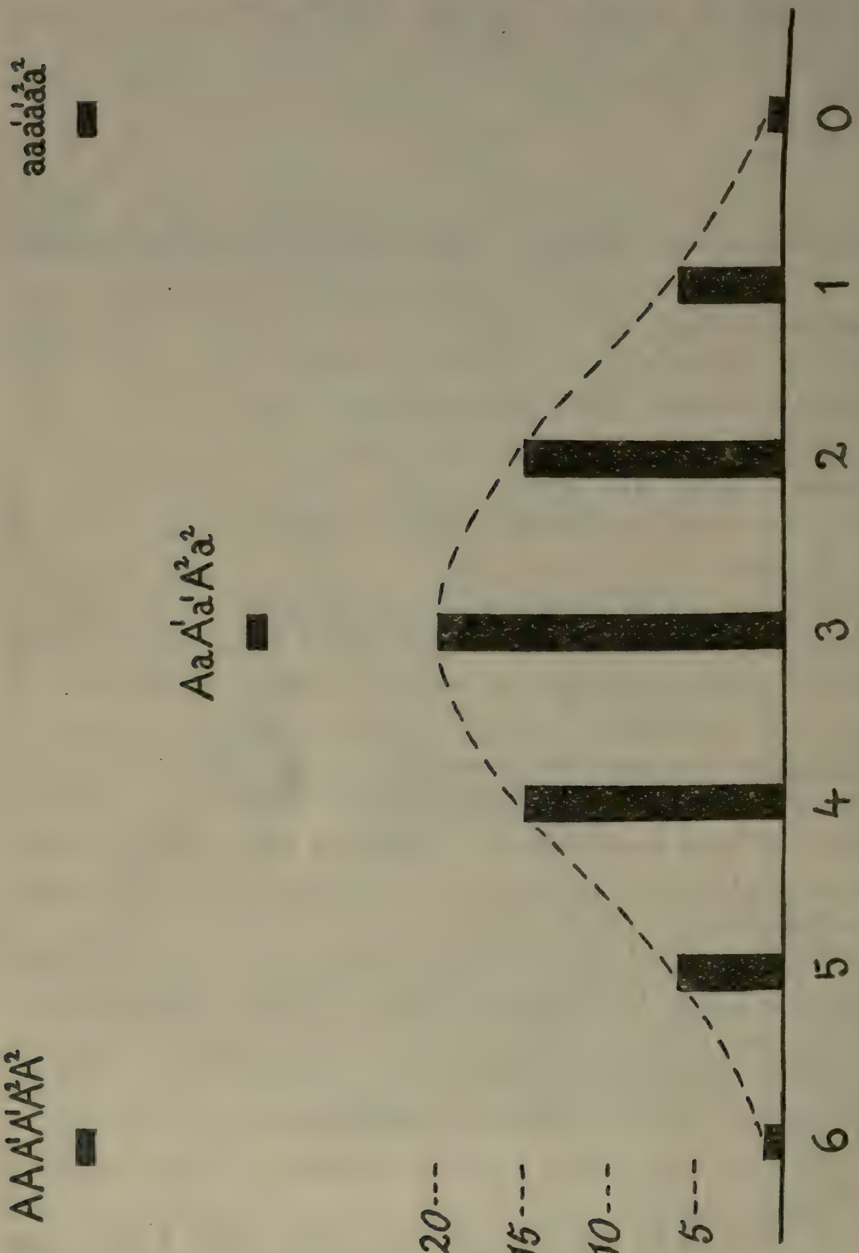

FIG. 9.—For explanation, see text.

contains none of them. The first cross contains a single dose of each of the three factors and is, on hypothesis, exactly intermediate in size between the two parents. Such an animal,

from the standpoint of our discussion, forms four kinds of gamete, viz. (1) those containing all three factors; (2) those containing any two of them (whether $A + A^1$, $A + A^2$, or $A^1 + A^2$ does not matter); (3) those containing but one; and, lastly, those containing none. Further, these four types of gamete are produced in the ratio 1 : 3 : 3 : 1. When two such series of gametes are brought together by mating the first-cross animals with one another, it is easy to calculate that seven different kinds of individuals are formed according as they contain six or less doses of any of the three factors. In point of size they will form a continuous curve (Fig. 9) of which the extremes are identical with the weights of the original parents, and the mean is that of the first crosses.

On the whole the phenomena observed under experimental conditions are similar to those expected on the hypothesis just outlined. In the case of our poultry, for example, Major Bailey and I showed that the observed phenomena could be explained on these lines, in terms of four factors. There is of course a further test. Certain of the individuals in the F_2 generation must be homozygous for either one or two or three of the postulated factors. The extremes must clearly be in this condition, and among the others homozygous individuals should occur in each of the two classes of 15. In actual experiment, testing for these homozygous intermediates would be a hopeless task to enter upon. Nevertheless, if the hypothesis is to serve as an acceptable basis for future work, we ought to be able to test it by breeding the more easily identified extremes together, and by showing that strains breeding true to intermediate size can be produced. In the case of the Sebright, Major Bailey and I showed that the small F_2 birds breed true, and I have now some evidence which seems to make it fairly certain that a constant strain of intermediate size can be formed.

The hypothesis of multiple factors, then, presents a view of these cases of quantitative variation which goes some way towards bringing them into line with cases in which the hereditary characters are of a distinctly qualitative nature. But before we can regard this interpretation as more than

a hypothesis a great deal of laborious experimental work will have to be carried through.

Nor must we forget that there are distinguished students of genetics who look at the matter from another point of view. Chief among them is Professor Castle, who bases his opinion mainly upon a very extensive and valuable series of experiments dealing with the inheritance of pigmentation in the coat of rats. In this species there is a pattern form known as "hooding." In a typical hooded rat the head and fore part of the body are pigmented, while a pigmented stripe runs along the back and includes the tail. The rest of the coat is white. The extent of the white area varies considerably. Starting with more or less typical hooded rats Castle made two main series of experiments. In the one he selected out and bred from those animals which possessed the greatest amount of pigmentation; in the other he used animals which showed most white. In each case the process of selection was carried through sixteen to seventeen generations, the end result being that two strains were established, of which one showed a very much greater pigmented area than any of the original rats, while in the other strain the amount of white was greatly increased.

Castle further claims that when the selective process is reversed either strain can be brought back to the original state of pigmentation at about the same rate as that at which it departed from it. Now the hooded character behaves as a simple recessive to self-colour when crosses are made between these two forms. Consequently Castle considers that a single genetic factor can undergo quantitative change under the influence of selection. The point here at issue is one of fundamental importance to all work where quantitative characters are involved.

Castle's views have not escaped challenge from other genetic workers. In America, where people are much more alive to the importance of these things, they have become the subject of keen controversy. In their recent book on *The Mechanism of Mendelian Heredity* Morgan and his colleagues have examined Castle's results in some detail and have pointed

out that they are not irreconcilable with the hypothesis of multiple factors.

For some years past I have been working at a case in rabbits which is not dissimilar to that of Castle's rats. It is another case where we are concerned with the extent of white in the coat. The Dutch rabbit is characterised by a well-marked pattern as regards the distribution of the white and pigmented areas. Such rabbits not infrequently throw what the fancy calls wasters — animals in which there is a considerable amount of irregular white patching on the pigmented area. From animals of this type I have succeeded in establishing a strain of rabbits which is almost completely white, and breeds practically true. When crossed back with the Dutch form the offspring are intermediate in appearance. Such intermediates, mated together, produced not only intermediates but also young of the two extreme forms—some like the Dutch and others almost white. My results as yet are not sufficiently complete to attempt a formal scheme in explanation, but those already attained seem more in harmony with the hypothesis of multiple factors than with the view put forward by Castle.

Meanwhile the matter is of such fundamental importance for the solution of breeding problems involving apparently quantitative features like weight, size, yield and so forth, that further experiments with different material ought to be undertaken at the earliest opportunity. Only in this way can we hope to disentangle the many issues wrapped up in the term selection, and to place the operations of the practical breeder upon a firm basis of ascertained and co-ordinated facts.

I have mentioned but a few of the lines of inquiry which at present are attracting the attention of the student of genetics. There are others equally far-reaching and only less developed because younger in point of time.

There is, for instance, that concerned with the viability or non-viability of particular forms of zygote. The yellow mouse is a case in point. Yellow is dominant to other colours such as agouti, black or chocolate. But all yellow mice are heterozygous for the yellow factor. Yellows bred together

give yellows and non-yellows in the proportion 2 : 1, instead of in the normal 3 : 1 ratio. Extensive breeding experiments led to the conclusion that the homozygous yellow was formed but that it died at an early stage during the embryonic development. Quite recently this deduction, made from purely genetic work, has been confirmed by several American workers, who have looked for these early embryos in the uterus and found them dead. Factors affecting the viability of the offspring have also been demonstrated by Morgan and his co-workers with Drosophila, and it is not unlikely that they will play an important part in the future of animal breeding.

Again, the study of variegated plants has already led us to the conception of individuals made up of components belonging to different races. Plants have been produced of which the inner core is that of the tomato and the outer skin that of the black nightshade—or the position of these two species may be reversed, with a resulting plant quite different in form. To-day they are but the curiosities of the laboratory, yet who can say whither they may lead us to-morrow ?

Nor should mention be omitted of those fascinating studies which treat of the action of external influences upon the germ cells themselves. Hertwig has shown that the sperm of a frog exposed to the influence of radium may lose its function of hereditary transmission and yet retain its power of stimulating the ovum to develop. Parthenogenesis, even among the mammals, is brought within the bounds of possibility.

For the practical breeder this playing with the germ cell may be fraught with significance. To-day we are limited in our researches by the number of different kinds of germ cells in the world. The making of a new creature means the union of germ cells that have not previously been brought together. We can make use only of such as already exist and can enter into combination with each other. For fresh combinations we must have fresh kinds of germ cells. When we understand more of their architecture we may one day be able to make them, whether through the influence of radium or of some other physical or chemical agency. Out of some wild labora-

tory experiment may one day flow a stream of new forms of living things.

But we are getting into a region of speculation hardly to be justified even by the title of this address. Though these things come to pass and some of us be willing to sing our *Nunc Dimittis*, I doubt whether Presidents of Boards of Agriculture will ever be among the number. Their salvation lies along other paths. It is for us poor servants of research to help to smooth their way as best we can. Let us then consider for a few moments this study of genetics in its purely utilitarian aspect.

To an audience like this it is unnecessary for me to dilate upon the necessity of accurate knowledge adequately presented. The spirit of research is to a modern civilisation what oxygen is to a living tissue. Without it there must inevitably ensue decay and ultimately death. If, as a nation, we have not yet learned this lesson, we are doomed. I am going to assume that we have learned it, and that, in the future, research in genetics, as well as in other branches of science, is not going to be hampered and stunted merely through lack of material means. Essential as these are, even more essential are the men. And they are very much more difficult to find. Every young man who starts off to do some research work is not necessarily endowed with the true spirit of investigation. Only too often he is attracted by the novelty of the thing, by the pleasure of playing with new and unfamiliar tools. For the great work that is to be done it is the born investigators that we want, the *rari nantes* whose hearts are in it, who refuse to be sucked down by the swirling inducements of life.

Huxley once said that "if the nation could purchase a potential Watt, or Davy, or Faraday, at the cost of one hundred thousand pounds down, he would be dirt-cheap at the money." Since that was written we are all unhappily aware of the great fall in the purchasing power of money. At the same time the machinery of to-day transmutes knowledge into commodities so very much more rapidly that I have no doubt Huxley would have multiplied his valuation many times

over had he penned that sentence forty years later. I do not wish to imply that a Faraday is to be had even for a million pounds to-day. I only wish to emphasise Huxley's point, that a first-rate intellect is cheap at any price you are asked to pay.

I would suggest that the President of the Board of Agriculture keep a watchful eye upon the Universities and be prepared to purchase these first-rate intellects whenever they appear. They are not common. Like old masters they come irregularly upon the market. A period of years may go by without one, and then suddenly a single year may throw up several. Some elastic system is needed which will allow of their being captured whenever they chance to appear, and provided with ample resources for doing the work they wish to do, which they alone can do. Given the right men and given the resources I have no fear of the result, even as judged by the purely utilitarian standpoint.

Take wheat alone. Biffen's work has already added hundreds of thousands of pounds yearly to the wealth of this country. Howard, in India, has produced a new wheat which is now spreading over the Central Provinces and is expected shortly to increase the annual value of the crop in that area alone by £7,000,000. The experiment station in Ohio is supplying the farmers of that State with a wheat that produces on the average an increase of two bushels to the acre on those previously grown. With two million acres under this cereal, the gain is obviously considerable.

These are but trifles compared to what could be done in the near future if but a few hundred skilled brains could be persuaded to study the genetic properties of plants and animals. Every year, in the British Empire alone, tens of millions of potential wealth, the ingathering of which would require no greater expenditure of labour than at present, are being thrown away. It is true that a start has been made in a timid fashion. We find an experiment station here and another there, carrying out genetic work as best they may, generally with scanty staff and often with inadequate means. But one would have thought that the very success of these

stations would long ago have brought the authorities to realise what is possible on a larger scale.

To any one of average intelligence the practical outcome of Mendel's discovery has been obvious for more than a decade. I confess that I have often been struck with amazement that, with one notable exception, not a single statesman in this country seems to have had imagination enough to give the subject even a thought. Even to-day, when there is so much talk about the development of the resources of the Empire, it is strange that no attention has been directed to a source of wealth so colossal in extent and attainable through such simple and obvious means. Let us hope that this period of ignorance in high places is now past, and that investigations, which are bound to lead to such enormous additions to our national resources, will in future be fostered and encouraged.

Suggestions as to how this is to be done, as to the way in which the Science of Breeding is to be given a future worth having, would carry little weight from an academic person like myself. But while the great ones nod it is surely permitted to the student to dream, and it is with a brief account of such a vision that I would conclude what I have to say this evening.

I saw before me a great place where men and women were making and imparting knowledge, but it was the making of knowledge to which they seemed to give most thought. And perhaps because my interests lay chiefly in the subject of genetics, it was in those parts of the place where such studies were pursued that I came to find myself. There were acres of gardens hedged around with yew and other evergreens. In each one of these gardens there was growing a different manner of plant. One garden was given up to all sorts of peas, another to the various kinds of bean, another to sunflowers, and so on. I was told that this was the great collection of the varieties of valuable plants that would grow in the country. It was to the breeder what his stock of pure reagents was to the chemist.

Each garden, I learned, was in charge of one whose business it was to devote his or her life to the particular plant that it contained. By the gardens, too, were houses where these people lived, so that they might at all hours be among and

learn about the plants they tended and worked with. And here and there were laboratories where each worker had an allotted place. Glass-houses there were also where these were required. Further, they told me that in another land across the equator there were gardens where in winter they could grow the seeds that had ripened in the summer, and thus have seeds of a further generation to sow in the following spring. In this way they could accomplish in one year the work that would otherwise take two years to perform.

When any of them had made a new plant that seemed of value it was tested by being grown in larger quantities on farm lands near by. And if it proved to be better than those which existed before, it was eventually distributed through the State farms to growers all over the country. Nor was the labour of him or her who made it forgotten, for it was held that an addition to the wealth of the State was deserving of reward.

There were many trees near the gardens and I was told that there were workers upon these also, who had made new kinds, growing faster and producing better wood than those from which they had started. Posterity, they said, would benefit from these more than themselves, but they held that they had a duty towards those that came after them, seeing that they themselves owed much to those who had gone before.

Leaving the garden plots, I wandered to a group of scattered buildings which I found to be houses for the breeding of small animals and birds. Here, as with the plants, were preserved the purified strains which had resulted from the labours of earlier workers. They were the standard reagents which might at any time be required for unravelling special problems. Here also were laboratories for those who devoted their time to understanding the physiology and pathology of the domestic animals. Beyond was a wide tract of farmland, where the larger animals, sheep and swine and cattle, had their quarters. Nor should I forget to mention the library and the meeting-hall where the many workers constantly gathered together for the discussion of the new knowledge which they or others had discovered.

Then, knowing something of the cost of these things, I asked one by me how it came about that they could obtain the money for all this work. But he only laughed, saying that even if the cost were ten times as great it would be as nothing in comparison with the wealth that they created. Had I not yet learned, he asked, that knowledge was the ultimate source of wealth, and that the chief thing was to obtain the knowledge, for when once that had been gained, the application of it would take care of itself. And you must know, he went on, that knowledge is not only created here but it is also disseminated. This country is but a small portion of a great world state, though for this branch of learning the place you see before you is the centre or brain. It is in the closest touch with many lands, in all parts of the world, that are linked to it in one great system. From them flows a constant stream of students hither, to learn from us and to be trained in our methods. Later they return whence they came and apply themselves to the betterment of the products of their own lands. These, however, are not the only students who come to us. We have long recognised that the stability of a state depends largely upon the extent of the knowledge spread out among its citizens. Social unrest and disorder have their springs in ignorance, and men are most often discontented when opportunity is withheld from them of attempting to perform those things of which in reality they are often incapable. Our system of education aims at instructing all our citizens in the natural history of man, and in the diversified nature of the population of which each one forms a part.

When a man knows enough to realise in good time the inevitable limitations with which he was born into the world, he is more likely to settle down and become a valuable and contented member of the community. To this end it is part of our duty to train chosen teachers, whose business it is to spread over the whole country the knowledge which we gather together, and especially such parts of it as affect our conceptions of the nature of man himself. Nor is the task so difficult as at first sight it might appear. For in the growing mind there is a craving for the knowledge of reality—an instinct to provide itself with

a sheet anchor ere it sets forth on the voyage of life, of which it presages dimly the perils and the storms. In days gone by men attempted to equip the children with sheet anchors ready made, with religion, with patriotism, and so forth. But the history of states has shown that in this world such things are no substitute for a knowledge of what is real, and it is upon that basis that the fabric of our state is built.

In such terms my informant spoke to me, telling me many strange things about a state greater than any in the world to-day. But whether the language of this state was English, or German, or some other tongue—to learn this was not vouchsafed to me.

VIII

OUR FOOD FROM THE SEA

By W. A. HERDMAN, LL.D., D.Sc., F.R.S.
Professor of Zoology in the University of Liverpool.

VIII

OUR FOOD FROM THE SEA

Our food from the sea, barring a few minor products, such as the delicious and nutritious "carrageen" jelly made from the Alga *Chondrus crispus*, is in the main obtained from our great commercial sea-fisheries, the discussion of which in their scientific aspects is a very large subject obviously only to be outlined, with a few examples of different methods of investigation, within the limits of a single lecture. It is scarcely necessary to emphasise the vital importance of our sea-fisheries. The harvest from the sea was never of more importance to the nation than it is now and probably will be for some years after the war. The sooner all classes of the population learn to appreciate the value of fish as a highly nutritious food the better it will be for the welfare of the community, and the greater will be the encouragement to those concerned in the industry to use their best endeavours both to increase the supply and to make the best possible use of it by preserving the produce so that nothing be allowed to go to waste.

There is still much to be done in the two directions (1) of exploiting local and periodic coastal fisheries and discovering the best methods of making available for future use what cannot be consumed at the moment; and (2) of educating the public to overcome prejudice and make a fuller and more systematic use of unaccustomed but excellent fish-food, such as, for example, the summer-caught, rich-in-fat herring cured in brine as a winter food. I shall have more to say farther on as to the value of such salt herring as a source of fat, highly desirable under present circumstances.

Most people have very little idea of the magnitude of our British fisheries, and of the rate at which they were increasing of recent years—before the war—or of the predominating position to which our fishing fleets had attained.

In 1914 our fisheries made up nearly one-half of the total for all countries of North-West Europe, and nearly 70 per cent of the North Sea fisheries alone. The total produce of our sea-fisheries has more than doubled in the last quarter of a century, and the average of the last few years before the war amounted to over a million tons (about 23,500,000 cwts.), bringing in about £15,000,000 when landed, and valued at probably three times as much, say nearly £50,000,000 sterling, by the time it reached the consumers.

This great increase in the amount of fish brought to our markets has been due to improvements in the boats and in the methods of fishing, and to an enormous extension of the fishing grounds. The picturesque old sailing trawler of Brixham, working in local waters with a small beam-trawl, has developed into the ugly but highly efficient modern steam-trawlers, equipped with huge otter-trawls and making lengthy voyages to Iceland and the White Sea in the north or the Canaries and the coast of Morocco to the south, conducting their operations, in fact, over an area of more than a million square miles and down to depths of 200 fathoms.

All this applies to the time before the war. We know how splendidly the men of our fishing fleet have responded to the call of duty, and the invaluable service they have rendered in patrolling our home waters, in hunting down submarines and in constant mine-sweeping during recent years. It is supposed that about ten per cent of our fine steam-trawlers and drifters, and their gallant crews, have now been lost. Their place will not be easy to fill.

As a natural result of the war conditions the produce of our sea-fisheries has dropped to less than a third of what it was: the total catch during war-time has averaged about 7,000,000 cwts. per annum. Very many millions of fish have therefore been left uncaught in the sea to grow and propagate, and it is an interesting speculation whether this unforeseen and

undesired experiment in the restriction of fishing, on an enormous scale, will result in the re-stocking of depopulated grounds such as the "Dogger Bank," and give rise to greatly increased fisheries in these home waters after the war.

Turning now to the chief kinds of fish caught, they may be divided for practical purposes into the "round" and the "flat" fish. Round fish are those—such as cod, herring and salmon—where the body is more or less circular in cross-section, while flat fish include the equally familiar soles and plaice, with flattened upper and lower surfaces. Amongst round fishes there are two groups of primary importance, those related to the cod (*Gadidae*) and those of the herring tribe (*Clupeidae*). The former include :—

Hake, a southern fish forming the greater part of the catch off the south of Ireland, in the Bay of Biscay, and southwards to Morocco.

Haddock, a northern fish forming nearly half the total catch from the North Sea.

Cod, a northern fish very abundant north of the British area, around the Faroes and Iceland, etc.

Whiting, abundant in the North Sea and generally around our coast.

Ling, a northern fish, abundant on the west of Ireland, Scotland and farther north.

The herring family (*Clupeidae*) includes the sprat, the pilchard (the young of which is so familiar in the preserved form of "sardines"), the anchovy and, most important of all, the true herring. All these Clupeoid fishes are noteworthy for the relatively large amount of fat they contain in the form of minute globules of oil disseminated through their flesh, while the cod and its allies are almost destitute of fat. The herring, however, has a very different amount of fat in its composition in different states and at different times. For example, the winter herring in poor condition may have only 4 or 5 per cent of fat, while the spawning summer herring may have from 30 to 40 per cent. The average of three series of Manx herring, caught in the summer of 1917 and cured in brine, gave

the following analysis,[1] and may be contrasted with the composition of the cod :—

	Herring.	Cod.
Fat	22	0·3
Proteid	21	16·7
Ash (+ salt)	9	1·3
Water (+ traces)	48	81·7

Other Manx herring, however, caught in September 1917, cured in brine and analysed in winter, gave as much as 32·72 per cent of oil (fat).

It is this relatively large amount of easily digestible fat in the flesh of the herring that gives this fish its special value as a winter food, and no effort should be spared to increase the home consumption of herrings. They are probably the cheapest form of animal food and have a very high nutritional value. Many people will be surprised to learn that out of 12 million cwts. of herring landed, nearly 10 million cwts. were exported annually before the war. The total catch is far from being too much for the needs of our own country. Taking three herrings to the pound, the total catch in the United Kingdom before the war would only allow two herrings a week to each adult individual of the population.

The flat fish of our markets (with the exception of skates and rays, which are a totally different kind of fish and are nearly related to dogfishes and sharks) belong to the family *Pleuronectidae*, the members of which undergo a remarkable transformation in their early life-history, whereby the bilaterally symmetrical larva, with the right and left sides of the body similar and an eye on each, undergoes in its growth a torsion of the head and some other parts, a flattening of the body from side to side, and a great extension dorso-ventrally so as to be converted into the familiar "fluke" form, with the upper (usually the *right*) side of the flat body pigmented and bearing both eyes, and the lower blind and more or less non-pigmented or white. Our best-known marketable Pleuronectids are :—

[1] By Dr. James Johnstone of the University of Liverpool (see for further details *Lancashire Sea-Fisheries Laboratory Report for 1917*).

Halibut, a northern fish of large size.
Sole, commoner in the south down to Morocco ; a shallow-water fish common in the Irish Sea.
Turbot, in deeper water ; a North Sea fish, but not very abundant.
Brill, more abundant than the Turbot, especially in the south.
Plaice, a northern form, very abundant on the coasts of Iceland and farther north, distributed all around our coast and important as a food of the people.
Flounder, of less importance ; especially abundant in estuaries.

It is in connection with some of these more sedentary flat fish that depletion of certain fisheries has been most clearly established, or, to put it more cautiously, that it is felt that there may be risk of the fishery being depleted on certain grounds. The more widely roaming herring, mackerel, cod and haddock are probably safe from man's ravages ; but the more local, bottom-haunting sole and plaice are less independent and more at the mercy of their immediate environment, including the fishing fleet. It is therefore in connection mainly with such fish that attempts have been made in the United States and several European countries to compensate for the ravages of the fisherman by artificially hatching and rearing young flat fish to add to the stock in the sea.

One of the most important and practical questions in the whole range of marine zoological investigation is : Can we increase the yield of our fisheries by cultivation ? We can cultivate shell-fish, such as oysters, mussels and cockles, on the seashore with much profit. Can we do anything towards farming our inshore or offshore fishing-grounds ? The fisherman at present is a hunter of the fish, can we reasonably hope to make him in time a farmer, reaping a harvest that in part at least he has sown ? These are the ideas that have led to the hatching, rearing and transplanting operations which are carried on with more or less energy and success in various parts of the world.

It is by no means easy to determine whether the artificial hatching of sea-fish has as yet had any effect upon any local fishery. It is not possible to mark or brand your larval fish from the hatchery so as to recognise them when caught as

adults ; nor is it practicable to devise the control experiment of both adding to and not adding to the same fishery, or two exactly similar fisheries, simultaneously, so as to secure comparable results. But it may be pointed out that much help may have been given to a depleted fishery although no effect is noticeable. The condition of the fishery might have been worse had no artificial help been given.

When one thinks of the enormous numbers of eggs produced naturally, in a season, by most of our common fish, as shown in the following list, one is inclined to fear that the comparatively small number of millions, or even of hundreds and thousands of millions, of young fish turned out from hatcheries will be of little avail, and may amount to nothing more than the proverbial " drop in the bucket."

The average number of eggs spawned by a single female fish in the course of one season is :—

In the Ling	18,500,000
,, Turbot	8,600,000
,, Cod	4,500,000
,, Flounder	1,000,000
,, Sole	570,000
,, Haddock	450,000
,, Plaice	300,000
,, Herring	32,000

But probably a truer conception of the state of affairs is obtained by reflecting that while countless millions are produced, countless millions also perish each season from natural causes (as opposed to man's operations)—that is, from their natural enemies and other adverse influences in the environment. As eggs, as embryos, as larvae and as post-larval young fishes, they are the food of most of the larger animals around them in the sea. Probably only a very few out of each million reach maturity, and it is out of that scanty remnant that the fisherman takes his toll and so may in some cases " over-fish " a limited area so as to reduce the population below its power of recovery. The enormous numbers produced do not, then, necessarily mean an enormous rate of increase, but they may afford man his opportunity to step in,

and by adding some millions from his hatchery do something to repair the damage and avert or delay the destruction of a local fishery.

It may be pointed out further that even though the young fish, such as plaice, are turned out to sea soon after being hatched, say about the time of the absorption of the food-yolk, they have been protected from their natural enemies during some three or four weeks at least—about half the time from the egg to the metamorphosis—and that moreover is the period when, as eggs, embryos and young larvae, they are most feeble and defenceless, and most in need of artificial protection.

We find at the Port Erin hatchery that, although the periods of embryonic and larval life vary to some extent—probably with the temperature of the sea-water—the average times are as follows, in the case of the plaice :—

Embryo, from fertilisation of egg to hatching, in February, 24 days.
Embryo, from fertilisation of egg to hatching, in March, 22 days.
Embryo, from fertilisation of egg to hatching, in April, 20 days.
Larva, from hatching to absorption of yolk, about 7 or 8 days.
Post-larval, abs. of yolk to metamorphosis, 28 to 40, say 34 days.

The most significant work, and most interesting experiments in connection with artificial operations, have been carried out by the United States Bureau of Fisheries and by the Fishery Board for Scotland. One example may be given from the work of each of these organisations. It has been long recognised that if a species of fish could be introduced into an area where it was previously unknown, that would be satisfactory evidence of the success of artificial operations, and the United States Bureau has shown in its successive Annual Reports of the Commissioner of Fisheries that by collecting and hatching the eggs of the shad (*Clupea sapidissima*) on the Atlantic coast, and setting the larvae free in the Pacific, in the neighbourhood of the Sacramento River, a profitable shad fishery has been established on the Californian coast. The last report published shows that in 1915, the latest year for which statistics are completed, the Pacific shad fishery yielded over

seven and a half millions of pounds, valued at over 75,000 dollars.

The Fishery Board for Scotland carried on for some years an interesting experiment in adding artificially hatched plaice larvae to a circumscribed sea-area (Upper Loch Fyne), with the view of determining whether an increase was noticeable in the number of young fish present. Positive results seem to have been obtained. During a period of six years millions of larvae were hatched at Aberdeen and deposited in Loch Fyne, and during the next six years none were added; while during the whole period of twelve years experimental hauls of the net were made on certain selected beaches where the young metamorphosed plaice congregate. The statistical results show that during the years when larvae were added the number of young fish caught, per hour of fishing, was more than double the number caught in the succeeding period of six years. Or, to put it another way, the figures given in the Report show that the addition of about twenty millions of plaice larvae a year doubled the number of young metamorphosed fish on the shallow beaches of Loch Fyne.

It has sometimes been said that the young fish turned out from hatcheries may possibly be weaklings, which on account of having been reared under artificial conditions may die in their early youth, perhaps even before undergoing metamorphosis. Experience shows that all such fears are groundless. In the hatchery at the Port Erin Biological Station young plaice have been reared up to their fourth year, when they had become sexually mature, and had, a year before, in their turn produced spawn for the hatchery. Last year (1917) there were three generations of plaice living together in the institution — the grandparent spawners which had been originally wild fish, the parents which were hatched in the spring of 1914 and were then spawning (in March 1917), and the young of the third generation which were developing as normal larvae. This year again (March 1918) some of the fish hatched in 1914 have produced fertile spawn—there can be no doubt that they are perfectly normal, healthy fish.

Apart from these and many other experiments in practical fisheries exploitation and cultivation—in which the United States of America have certainly led the way—all modern scientific fisheries research is directed towards finding out the conditions under which our food-fishes live, feed, migrate and reproduce their kind, so as to determine the possibilities and methods of preserving them from destruction, increasing their number and even predicting when and where profitable fisheries may take place. Marine zoologists and other men of science in practically all civilised countries are gradually building up by their observations a science of the sea—Oceanography—which, although it involves physico-chemical problems, is largely a matter of biological investigation with very important bearings on fishery questions.

As an example let us take the investigation of the ultimate food-matters of the sea, a very large subject in itself. The fishes that we eat, such as cod, plaice and herring, feed upon other animals, and these upon still smaller living things. The plaice is a bottom feeder living chiefly upon cockles and other molluscs, which in their turn feed upon Diatoms, lowly microscopic plants which are present in enormous profusion in sea-water at certain times and places. The cod is almost omnivorous, but a favourite food is evidently the larger Crustacea, which again feed upon smaller invertebrates, and these—with perhaps some intermediate stages—upon the Diatoms.[1] The herring feeds mainly upon Copepoda, small, somewhat shrimp-like Crustacea, which, like the Diatoms, may be present in the water in enormous abundance; and there is some evidence to show that the shoals of herring which constitute a fishery may be following and feeding upon special swarms of Copepoda. At the time of the summer herring fishery off the Isle of Man in August 1917 the fishermen themselves noticed that they were catching the fish in greatest abundance in the neighbourhood of large discoloured patches of water containing innumerable reddish specks. They brought a bucket of this water ashore to the Port Erin Biological Station, where the

[1] There are other still smaller organisms in sea-water, but I take the Diatoms as a type of all the micro-phyto-plankton.

red specks were examined microscopically and determined to be the Copepod *Temora longicornis*, while an examination of the herrings caught at the same time—and for days later—showed that their stomachs were crammed full of a reddish mush which microscopic examination showed to be the partially digested bodies, legs, tails and other parts of the same Copepod.

Other similar cases have been demonstrated; and Dr. Allen, at the Plymouth Marine Laboratory, has shown that mackerel fisheries in the English Channel are connected with swarms of the Copepod *Calanus finmarchicus*, and that Copepod with the prevalence of sunshine—an intermediate link being probably the Diatoms upon which the *Calanus* feeds and which depend upon the energy derived from sunlight for their nutrition.

The herring and the mackerel, then, get their abundance of fat—their oily flesh—from the oil globules which are so abundant in their food, the Copepoda, and the Copepoda manufacture their oil and other substances from the Diatoms and other minute organisms upon which they feed, while the Diatoms, being plants, build up their living protoplasm by photosynthesis from simpler inorganic substances, getting their carbon, for example, from the carbon dioxide in the sea-water. As on land, so in the sea, all the animals are ultimately dependent upon plants for their nutrition, and the plants are similarly dependent upon their inorganic environment. So far as regards organic food, the plants are the producers and the animals the consumers, and the pastures of the sea are no less real and no less necessary than those of the land.

A few years ago Professor Benjamin Moore carried out, at the Port Erin Biological Station, an interesting investigation on the variations in the alkalinity of the sea-water throughout the year, in which he showed that an increase in alkalinity is due to the relative absence or reduction in the amount of carbon dioxide present, and is really a measure of the conversion of inorganic carbon into the carbon present in the bodies of living organisms, and especially in the Diatoms which develop in enormous quantities in the early spring under the influence

of the increasing sunlight. The amount of this turn-over of carbon is probably in the neighbourhood of from 20,000 to 30,000 tons [1] per cubic mile of sea.

It was Sir John Murray who first suggested that the meadows of the sea—the Diatoms in the surface waters—like the meadows of the land, start to grow in spring simply as a result of the lengthening of the days and the increase in sunlight, and Moore's figures in regard to the resulting change in alkalinity show that the amount of carbon stored up in the growing vegetable matter in the sea is far greater, per acre, than is the case on land. Such considerations suggest at least the possibility that there is much more ultimate food matter in the sea than is at present made use of, and that a scientific aquiculture in the future may discover the means of converting more of the available carbon into fish-food, and then fish, so as to increase our marine harvest.

Scientific investigations bearing on sea-fisheries questions have hitherto dealt with the fish as they live in the sea—their structure and habits, their reproduction and life-history, their food and general relations to their environment—with the object of discovering the best means of conserving the fisheries or even of increasing the supply of fish. But it is now coming to be recognised that there is need also of biologico-chemical investigations on the fish after they are caught, on the post-mortem changes that they undergo in different circumstances, and on how best to preserve them with their nutrient and other desirable qualities unimpaired until they are put on the market and used as food.

Such investigations will teach us how best to deal with the occasional unexpected superabundant catches which glut the markets and sometimes result in much good food being wasted as field-manure. But they will also lead to a more equitable distribution and a more profitable use of the periodic profusion of such local fisheries as those of herrings,

[1] These figures are not final and may be subject to some correction, but they give an indication of the vast scale of the phenomenon and of the large amount of potential ultimate food-matter available.

mackerel and sprats. The best use, economically, that can be made, for example, of the summer herring fishery in the Irish Sea, or in the Hebrides, is to cure in various ways (kippering, salting, etc.) the great bulk of the catch. Distribution can thus be controlled, consumption can be spread over a longer period, the product may be improved as a food, and local industries established. As Dr. James Johnstone has pointed out, "a clamant need of the present time, and indeed of normal times, is the curing of summer-caught herrings for consumption in the winter months, when fat-rich foods are more useful than in the warmer months." [1]

Another example that may be mentioned is the winter sprat fishery in Morecambe Bay.[2] During the height of the fishery last winter fully seventy tons of fish were landed each day, and the value to the fishermen of such a catch was over £300. A ton of sprats contains on the average 130,000 fish. In a day's fishing, therefore, nine millions of sprats may be captured, and this goes on day after day without making any appreciable difference to the abundance of the fish. The question has naturally occurred in connection with this and other similar fisheries elsewhere, whether it would not be desirable, with a view to a more perfect distribution and more economic utilisation of this food-product, to establish curing or canning industries for the purpose of converting the temporary superabundance of the fresh, perishable fish into a more permanent and highly nutritious article of diet. It is satisfactory to know that the matter is now being investigated from both the scientific and the commercial points of view, and that experiments are being made which, it is hoped, will lead to such preserving industries being established before the next fishing season comes round.

The United States Bureau of Fisheries, with its very extensive organisation and ample resources,[3] sets an example to

[1] *Lancashire Sea-Fisheries Laboratory Report for 1916*, p. 23.

[2] An interesting account of this fishery was given by Mr. A. Scott in the *Lancashire Sea-Fisheries Laboratory Report for 1915*.

[3] The last Annual Report of the Commissioner of Fisheries shows that the appropriations for the Bureau of Fisheries for the fiscal year 1917 amounted to \$1,144,850—about £230,000.

the civilised world in the promotion and utilisation of their important fisheries—both marine and fresh-water. Their experts seem to be equally successful in devising new methods and in conducting an active propaganda. The establishment of a new fishery, the provision of the necessary markets and the all-important demand on the part of the public are promoted simultaneously. The method seems to be to boom one fish at a time: in 1916 it was the Tile-fish, and in 1917 the Dog-fish, under a new name. Our European food-fishes have been known to the public for centuries, and their names, such as herring, cod and plaice, are very old; but the "tile-fish" is new to the markets, and the name is a recent invention. When, as the result of scientific exploration, the fish was found in quantity and introduced to the fishermen and the public, and it became necessary to find a name shorter than the zoological designation *Lopholatilus chamaeleonticeps*, the terminal part ("tile")[1] of the generic title was taken and is now firmly established in common use. When the fishery had been in existence for twelve months (1916) the known catch amounted to upwards of 10,250,000 pounds, valued at more than $400,000. During the fiscal year 1917 the tile-fish landed reached 11,641,500 pounds, and the receipts of the fishermen exceeded $477,730.

Having established this fishery, the Bureau then entered on a campaign to convert one of the most destructive and neglected fishes of the Atlantic coast, the spiny dog-fish, into a valuable asset; and the first step taken was to suggest a change in the name of the fish for trade purposes. We are told that people in all parts of the country will eat "cat-fish" but are prejudiced against "dog-fish," so the Bureau altered the name of the latter to "gray-fish," which "is descriptive, not preoccupied, and altogether unobjectionable."[2] There was apparently at first much prejudice and opposition to be overcome, but the Commissioner tells us that "an early feature of the campaign was the complete change in the fishermen's attitude after they had become fully informed as to the

[1] And possibly also because of the tile-like markings on the head.

[2] Commissioner's Report for 1917.

Bureau's plans ; and the autumn of 1916 witnessed the extraordinary sight of New England fishermen going out specially for gray-fish and selling their catch at remunerative prices for food." It soon became evident that the demand far surpassed the supply. The canned fish met with a ready sale and were soon all disposed of, as " the goods proved to be not only one of the best canned products on the market, but also one of the most economical to the consumer, who could buy at retail for 10 cents a can containing 14 ounces net weight of fish." Again, " although the canned product had been known to the trade and public only since October, in April 1917 it was known to be handled by dealers in 128 cities and towns in New York and Pennsylvania alone, and by May the fish was on sale by retailers in thirty states, and the District of Columbia."

Many other instances of the energetic and successful exploitation of American fisheries—in the interests both of the fishermen and the public—might be given, but these two examples, both bearing newly coined names which have rapidly become familiar to the public, must suffice.

There are many minor industries round our own coasts, such as the Morecambe Bay sprat fishery mentioned above, that would well repay further investigation—both scientific and commercial. It is probable that much more use could be made of our shallow coastal waters and our comparatively barren shores between tide-marks than is the case at present. Let me take one example from shell-fish cultivation—a large subject in itself. Any one who has tramped up the west coast of France visiting the various fishing centres will remember the prosperous oyster industries at Arcachon, Marennes, Le Croisic and Auray, and the extraordinary development of mussel-culture by the " buchôt " system on the mud-flats of the bay of Aiguillon. It seems difficult to find localities on our coasts where the French buchôt system could be worked successfully, but some experiments on the Lancashire coast have shown that transplantation of mussels from overcrowded beds to suitable ground not occupied by shell-fish may lead to greatly increased growth and a corresponding improvement in

the value of the fishery. The shell-fish industries of the west coast of England are of considerable importance, both as food and bait. In 1917 the returns in the Lancashire and Western District alone amounted to about two-fifths of the total for England and Wales, and the value to the fishermen was £40,000. There is probably no area of land or water that gives such a return in weight of food per acre as a mussel bed, and the shell-fish are eminently responsive to cultivation and capable of improvement. Here at least, if not yet in the open sea, we have an aquiculture comparable to agriculture ready to our hand.

To show what can be done at small cost to improve the value of shell-fish by judicious transplanting, the experiments made by the Lancashire Committee in 1903–5 may be recalled.[1] The work was carried out on the mussel beds at Heysham in Morecambe Bay, probably the most extensive mussel-producing grounds on the west coast of England.

In 1903 the Committee gave a grant of £50, to be expended on labour in transplanting overcrowded and stunted mussels which had ceased to grow to neighbouring areas not so thickly populated. The result was most striking. At the end of a few months the old, starved, undersized mussels—"blue-nebs," as the fishermen called them—had grown $\frac{3}{8}$ of an inch or more, and had reached the legal selling size. The animals inside the shell were in fine condition, and these mussels found a ready market at a good price. Shell-fish which in their original condition could never have been of any use as food had been turned into a valuable commodity at comparatively little labour and expense. The money value to the fishermen of these mussels that had been transplanted for £50 was estimated to have been at least £500.

In 1904, again, a grant of £50 resulted in the transplanting of some boat-loads of undersized mussels which were sold later on at a profit of over £500.

In the following year (1905) a grant of £75 resulted in the sale of the transplanted mussels some months later for £579.

[1] For the full details see the article by Scott and Baxter in the *Lancashire Sea-Fisheries Laboratory Report for 1905.*

On that occasion over 240 tons of the undersized mussels had been transplanted in six days' work. It was found that on the average the transplanting increased the bulk of the mussels about two-and-a-half times, and the increase in length to the original shell was in some cases well over an inch.

These experiments, on the industrial scale, were not carried further. The Lancashire Committee only desired to show what could be done and how to do it, and had no intention of running a commercial concern; but the results are very suggestive and encouraging as to what might be done in the further cultivation of our barren shores.

There are many other lines of scientific investigation and of practical exploitation of the sea-fisheries, the details of which cannot be given here. I shall be content if I have shown that something has already been done by zoological science for this great national industry, that much more still remains to be done both in the laboratory and in the field, and that it is all well worth doing with the object of increasing and improving our supply of food from the sea.

IX

TSETSE-FLIES AND COLONISATION

By R. NEWSTEAD, M.Sc., F.R.S.
Professor of Entomology in the University of Liverpool.

IX

TSETSE-FLIES AND COLONISATION

During the last twenty years or so rapid strides have been made in the science of Medical Entomology; in fact, nearly the whole of our knowledge of insect-borne diseases has been acquired during this relatively brief period, and the results have caused no little surprise both to the scientist and to the layman.

The principal vectors of disease are mosquitoes, sand-flies of the genus *Phlebotomus*, tsetse-flies, house-flies, fleas and lice, and the distantly related Acaridae such as mites and ticks. These and hordes of other blood-sucking creatures tend to make man's life intolerable, and the place in which he lives sometimes untenable.

The history of the movement in connection with the transmission of disease in both man and his domesticated animals by blood-sucking insects commences with the brilliant discovery, made by Sir Patrick Manson in the year 1878, that elephantiasis in man is transmitted by mosquitoes; and it is this discovery that has, in no small measure, been the keynote to all subsequent discoveries.

With regard to tsetse-flies and their effect on African travel, adventure and colonisation, let me say at once that this subject has not been singled out for exceptional treatment because the diseases which these insects transmit are either more general or responsible for a greater mortality among men and the domestic animals than other tropical diseases. So far as domestic stock is concerned, the mortality from tsetse-fly disease in certain portions of Africa is con-

siderably less than the mortality from such diseases as, say, rinderpest and East Coast fever. And the human mortality, so far as one can ascertain from official statistics, has averaged about 1 in 30,000 during the five years preceding the war. Clearly, therefore, it would be possible to show a higher mortality from other tropical diseases both among natives and among Europeans.

In 1908 and the two succeeding years cases of sleeping sickness were detected in Rhodesia and Nyasaland. "These cases occurred where the incriminated tsetse-fly of Uganda (*Glossina palpalis*) could not be the carrier of the disease, and attention was therefore directed to another tsetse-fly (*G. morsitans*), which was abundant in many parts of those countries, which was not limited to the neighbourhood of water, and which might be found wherever there was suitable shade. This discovery led to great apprehension among missionaries and other Europeans in those countries, and in 1911 appeals were made to the Secretary of State for energetic measures to be taken to combat the spread of the disease. As a result the Royal Society, at the request of the Colonial Office, sent out a Commission under Sir David Bruce." [1]

In 1913 Dr. W. Yorke and Dr. Kinghorn, of the Liverpool School of Tropical Medicine, discovered that the tsetse-fly (*Glossina morsitans*) of Rhodesia transmitted a trypanosome which produced a very virulent strain of sleeping sickness in man, and held that certain wild animals were in nature infected with the same parasite. These discoveries led to a general revival of the great interest which had previously been taken in tsetse-flies by colonists, zoologists and the members of the medical profession. These, I take it, are the considerations which induced the authorities of this University to include the subject of my lecture under the general heading of "Animal Life and Human Progress."

I will now proceed to define the general characters of a tsetse-fly, and endeavour to show as far as possible how to distinguish it from other members of its class.

The range of colour and pattern in tsetse-flies is not very

[1] *Rep. Inter-Depart. Committee on Sleeping Sickness*, p. 3 (1914).

FIG. 1.—Tsetse-Fly (*Glossina morsitans*), from a photograph of a living specimen. ×8.

To face page 211.

great, and several species are so strikingly similar in this respect as to render their specific determination a matter of great difficulty and doubt. On the other hand, a careful study of the male armature has revealed the fact that all the species hitherto described can be determined with comparative ease by a study of these appendages.

The general colour varies from dark brown or blackish brown to yellowish brown or dusky yellow. In certain species the abdomen is more or less uniformly dark brown or blackish (*Glossina palpalis*), in others yellowish brown with dark, interrupted transverse bands (*G. morsitans*), or dark brown with the first and second segments often paler (*G. brevipalpis*, etc.). The thoracic markings (see Fig. 1) are very similar in many species, but may be reduced to spots, as in *G. longipennis*; or the markings may vary *inter se* in a single species (*G. palpalis*). They vary in size, the smallest species being a little larger than a house-fly, the largest about the size of a queen bee (7-13·5 mm.).

The most salient characteristics of a tsetse-fly are (*a*) the long, thin proboscis, which, when at rest, is completely ensheathed by the spiny palpi, and (*b*) the unique venation of the wings, in which the fourth vein is curved abruptly upwards near the centre of the wing-area. Sexual dimorphism is well marked, the males being easily distinguished by the gibbose hypopygium at the apex of the abdomen on the ventral surface; in the females this structure is entirely wanting.

The life-cycle or mode of reproduction is unique among the members of the group (*Muscidae* = house-flies, etc.) to which the tsetse-flies belong, as the female, instead of laying eggs, gives birth to a single fully developed larva or maggot at intervals of a few days, given favourable conditions as to temperature, humidity and an efficient pabulum. During its intra-uterine life the larva is nourished by the secretion of specially developed glands; two moults take place, the effete skins being generally extruded with the fully developed larva during the act of parturition.

The larva is footless and rather faintly segmented, and when at rest its body assumes a cylindrical form. Its colour

is pale yellow, and the terminal segment is furnished with a pair of intensely black and somewhat hemispherical protuberances (the "tumid lips" of various authors, "ballonnets" of Roubaud), with a deep, cup-shaped pit or cavity between them. The paired stigmata of the respiratory organs open into the pit, and it has been held, until quite recently, that the protuberances or lobes function as a protection for the openings, thus forming a kind of air-chamber favourable to gaseous exchange during the intra-uterine life of the larva. Recent investigations[1] have shown that the lobes themselves are also provided with innumerable "air-holes" (about 500 pairs), and that these unique structures function only while the larva is maturing within the body of the parent.

Immediately after birth the larva buries itself in the earth or humus and rapidly undergoes its final change into the nymph or pupal stage. In this case the old larval skin is not cast off but is retained practically intact; it hardens rapidly and forms a protection or covering (puparium) for the enclosed pupa or nymph. The fly matures in about three weeks, and, in order to escape, breaks off the anterior end of the puparium by means of the frontal sac in a way precisely similar to that of the house-fly and other members of the *Diptera Cylorrhapha*.

In the year 1903, when Mr. E. E. Austen published his classical monograph of the tsetse-flies, only seven species were known to science. Since that date, however, nine additional species and four or five colour-varieties have been described, and it is highly probable that other species await the discoverer in the African continent.

These insects may be divided into three main groups, each group being clearly defined by the morphological characters of the male genital armature. In the *Glossina fusca* group the superior claspers are quite free; in the second group, of which *G. palpalis* may be taken as a type, the superior claspers are united by a membrane, but the tips of the claspers are free and widely separated; in Group III., *G. morsitans*, the

[1] *Annals of Tropical Medicine and Parasitology*, vol. xii. p. 93.

claspers are dilated distally and fused together in the middle line. A description of these appendages, together with photographic illustrations, was given at the lecture ; but as the prints cannot, for various reasons, be reproduced, further details need not be given, as it is difficult to visualise from descriptions alone.

The chief breeding-places are, broadly speaking, shady spots in the forest or along the shores of lakes and rivers. A favourite haunt of the pregnant fly is the under-surface of a fallen tree-trunk, or stout branch, which respectively are so placed that they do not quite reach the earth. Beneath the shadow of these the parent fly gives birth to a single larva or maggot, and the newly born creature immediately buries itself in the soil beneath. In such places large numbers of pupae are sometimes found, clearly the offspring of many different individuals, but whether the matrons congregate for this purpose is not clear ; such a trait is, however, common in the house-fly, and numbers of the latter, varying from half-a-dozen to thirty or forty, may be seen laying their eggs in a given spot which could be easily covered by the palm of the hand. Such places as I have indicated are the common breeding haunts of *Glossina morsitans* and *G. palpalis*. But the pupae of tsetse-flies have also been found in various other places ; in rot-holes, and between the great buttressed roots of trees ; in the ground under the petioles of palm leaves ; in the burrows of the great ant-bear, and in various other places.

The duration of the pupal stage may be given as three weeks, but much depends on the temperature and humidity. Much longer periods could be given.

Tsetse-flies, although very widely distributed over Africa, may be generally localised and confined more or less to "belts" or "zones." *Glossina palpalis* is met with most abundantly along the banks of rivers and the fringes of the great lakes ; on the other hand, *G. morsitans* often occurs in suitable places quite remote from water. In parts of Nyasaland with which I am familiar *G. morsitans* was not found to occur along the banks of the upper reaches of the Shire River, though an

apparently ideal type of vegetation occurs there in many places. Neither was it seen in the dambo or savannah or the thorny scrub beyond, but in the forest proper it was common and very widely distributed. The vegetation in the so-called "fly zone" in Nyasaland consists for the most part of typically "low forest," and in this respect is characteristic of that of the whole of the country. The relative density of the forest varies considerably; in some places the trees are fairly close together, but even so, small open areas are frequent, and much of the country is more or less park-like and generally flat, though slightly undulating in places. The tree which preponderates in this region is the Sanya or Ironwood tree (*Copaifera mopanie*, Kirk); in fact, it is so abundant that those portions of the forest in which it abounds are referred to as the "Sanya country" both by natives and by Europeans. In the dry season it supports a scanty foliage, and in the distance bears a striking resemblance to a small and rather lanky elm. The leaves, though hard and rather dry, are eaten extensively by the Impala antelope (*Aepyceros melampus*) and more sparingly also by other antelopes. Beneath such trees the land is generally clothed with short grass, which adds considerably to the park-like appearance of the country.

It must be distinctly understood, however, that there is not an unbroken line of Sanya trees. Many are the changes in the character of the flora even in relatively small areas. In places there may be a rather dense undergrowth of shrubs or scrub with an almost total absence of grass. Isolated clumps of trees, occupying the low mounds of deserted "ant-hills" (Termites), are quite a feature in some parts of the country, especially where the forest merges into the semi-dambo areas; such clumps, especially the older ones, often have a shade-giving undergrowth of straggling and non-deciduous shrubs, whilst the surrounding land may be clothed with the dwarfer kinds of grass. Baobabs too are often seen within the forest belt; ebony (*Diospyrus* sp.) is very common, but *Erythrina* sp. less so. The giant creeper (? *Landolphia* sp.), with its soft, cork-like tissues and serpentine

folds, climbs to the top of some of the taller trees, sending down long lianes and fruiting branches, and in August its beautiful pappus-bearing seed lies scattered over the land like giant thistle-down. It is one of the most grotesque as well as one of the most characteristic plants of the forest. In more open country one finds a leguminous tree in some abundance, its enormously long, pendulous fruiting pods hanging from its slender branches in great profusion. Antelopes eat portions of the pod, and grey hornbills and squirrels extract the small beans. There is some doubt as to its botanical name, but it is possibly a representative of the genus *Parkia*. A beautiful yellow-flowering Cassia (*C. goratensis*) grows in similar bush-like country, but is not very common.

In such country, and amongst such surroundings, the Impala antelope makes its home and the common tsetse (*Glossina morsitans*) propagates its species. Three things are therefore apparently correlative: the Sanya tree, with shady undergrowth, the Impala antelope and *Glossina morsitans*. In other words, "Sanya country" and "Fly country" are one and the same, and such also is the favourite resort of one of the commonest of the vertebrata in the Upper Shire. This, however, is but a *local picture of a portion of the fly area in Nyasaland*[1] as seen during the winter, when the tropical sun pours through the almost leafless trees, rendering the tenacious soil indurate and robbing it of all moisture. There is practically no humus, certainly no sand, and there is little else but sun-baked clay until the rains commence in October, when the land becomes plastic and fertile.

The food of tsetse-flies consists entirely of the blood of animals, chiefly that of the larger mammals and man, but sparingly also of avian and reptilian blood.

The natural enemies of these insects do not appear seriously to check their increase; in fact tsetse-flies seem to have struck a balance in this respect. A predaceous wasp (*Bembex forcipata* Handl.) stores her brood cells with these and other

[1] It is well known that *G. morsitans* occurs in other parts of Nyasaland where Sanya trees (*Copaifera mopanie*) are absent.

muscid flies. Several species of Hymenoptera are parasitic upon tsetse pupae, including two Mutillids and a few of the smaller Chalcidoidea. Birds prey upon them to a very small extent; and recently Dr. Lamborn has given us an interesting account of his observations on the capture of tsetses by dragon flies.[1]

The factors concerned in the dissemination of the diseases known respectively as sleeping sickness in man and trypanosomiasis (nagana, etc.) in domestic stock are:—

(1) Species of Trypanosoma; free-swimming, microscopic organisms which are found chiefly in the peripheral blood. These give off a toxine causing the death of the host. (Man and domestic stock.)

(2) Big game (antelopes, wart-hog, etc.). These also harbour the trypanosomes, but are tolerant of their presence. "Big game" therefore act as the natural reservoirs for the trypanosomes.

(3) The tsetse-flies. These are also tolerant of the presence of trypanosomes. A cyclical or partial development of the latter takes place in the gut of the fly. Tsetses are the chief and, so far as is known at present, the only vectors or disseminators of the disease.

(4) Man, who is generally non-tolerant and rarely survives the infection.[2] Man may form an important reservoir if allowed to remain in a fly-infected area. In the case of nagana, etc., domestic stock takes the place of man.

Trypanosoma gambiense is the cause of the disease in man known as "Uganda Sleeping Sickness." It is supposed to have been introduced from West Africa into Uganda at the end of the last century. In the epidemic which ravaged the native population between the years 1898 and 1906, some 200,000 people died of the disease. The tsetse which transmits the disease is *Glossina palpalis*.

Trypanosoma rhodesiense produces the Rhodesian and Nyasaland form of sleeping sickness, which would seem to be a much more virulent type of the disease in man than that

[1] *Bull. Ent. Res.* vol. vi. p. 552 (1915).

[2] A chronic form of the disease occurs in West Africa.

which is produced by the preceding species of trypanosome. The vector is *Glossina morsitans*.

Trypanosomiasis (nagana, etc.) in domestic stock is transmitted by several species of *Glossina*. It is impossible to keep stock in fly country, as the animals readily contract the disease and soon die.

The foregoing may be taken as a very brief summary of that part of my lecture which dealt with the morphology and bionomics of tsetse-flies. It is obvious, however, that these insects form a serious barrier in the way of settlement and of the opening up of new trade routes through fly-infested regions. There is need, therefore, of preventive operations, or the practical application of the facts which have been gathered from a careful and prolonged study of the diseases by many experts in various parts of Africa. These may be briefly considered under the following heads :—

1. *Clearing.*—I attach greater importance to this method, in *localised areas*, than to any other means which have been devised or recommended. Although the clearing of forest or scrub may not destroy the fly, one may safely say that the removal of vegetation such as is undoubtedly necessary for the existence of the fly would result in its complete banishment from the area thus treated. This method has been carried out in various parts of Africa, and there is abundant evidence to prove that clearings made in belts of forest frequented by *Glossina palpalis* have met with marked success. We have evidence to prove, moreover, that *G. morsitans* does not habitually occur in open spaces or in relatively open country, and to this I can abundantly testify from my own observations in Nyasaland. I maintain, therefore, that persistent localised clearing should be rigorously enforced throughout the whole of the fly-infested country, that is, in the immediate neighbourhood of populated centres or settlements and along the trade routes.

2. *Destruction of Flies in their Breeding-places.*—In view of the discoveries which have been made by various entomologists, the collecting of pupae, either by searching for them

in their natural habitat or by placing suitable trees as traps, would cause an appreciable diminution of the flies in small localised areas and in the immediate neighbourhood of the main roads.

3. *Destruction of Big Game.*—This very serious problem led the Colonial Office to form an inter-departmental Committee on Sleeping Sickness. In the Report issued in 1914 the following recommendations were made (p. 21): "Knowledge of the disease, its cause, and its remedies is still in the making, and hasty and imperfectly considered action of a drastic character, such as the attempt to effect a general destruction of wild animals, is not justified by the evidence before your Committee. On the other hand, your Committee recommend that until direct means of checking the fly have been discovered, the food supply of the fly and the chance of infection should be lessened in the vicinity of centres by the removal of wild animals, and that for this purpose freedom be granted to both settlers and natives to hunt and destroy the animals within prescribed areas, and subject to prescribed conditions."

Relaxation of the game laws in a country infected with tsetse was granted to natives in the prescribed areas in Nyasaland. In these districts, however, the natives seem to take little interest in game destruction, owing in no small measure to the fact that they have no very effective method of their own, and it would be most unwise, at this juncture, to supply them with arms of precision, even if there was a prospect of their using them when they got them.

4. *Medical.*—Before the advent of the great war the Colonial Office, the Royal Society, the Colonial Governments and other institutions sent out trained experts to investigate trypanosomiasis and its cause. Thus we find, among others, Sir David and Lady Bruce and their assistants engaged in Nyasaland; Drs. May, Yorke and Kinghorn in Northern Rhodesia; medical officers and others in Uganda and West Africa. These workers collectively have shown us how to combat the diseases in the light of our present knowledge. It is not too much to say, therefore, that through the efforts of these researchers great progress has already been made.

Our knowledge of the diseases and the causative agents has been greatly increased, the way of preventing their spread has been determined, and I have hopes that further research will enable us to suppress them altogether; thereby we may extend our colonies into the vast tracts of country which at the moment are clothed with forest and bush, forming the deadly haunts of the tsetse-fly and for the most part a barrier to the advancement of tropical agriculture and colonisation, and to the occupation by science of new fields of research.

INDEX

Acaridae, 209
Adapis, 111
Adaptation, 36, 37, 38, 39, 41, 42, 56, 57, 71, 110
Aepyceros melampus, 214
Algae, 93, 191
Allen, Dr., 200
Alosa finta, 72
nilotica, 72
Ammonites, 32
Amoeba of dysentery, 13
Amphimixis, 45
Anaemia, 136
Anaptomorphus, 111, 120
Anatomy, comparative, 33, 67, 108, 111
transcendental school of, 104
Anchovy, 193
Ancylostoma caninum, 152
duodenale, 151
Angel, 103
Animals, classification of, 102, 103, 104, 110
Ankylostome worm, 136, 151, 152, 153, 154
Anomia, 39
Anopheles maculipennis, 89
Anophelinae, 37
Antelope, 90, 214, 215, 216
Anthelminthics, 139
Ants, 84
Apes, 106-127, 130, 131
Appendix caeci, human, comparison with other Primates, 48
Arboreal man, 124
Archaetype, 104
Aristotle, 34, 46, 102
Assheton, Dr. R., 105
Aves, 32, 37, 66, 84, 85, 86, 88, 89, 215
Avicenna, 137
Baboon, 122
Bacillus, 86
Bacteria, 84, 92, 93, 147
Badger, 89
Bailey, Major P. G., 179
Baobabs, 214
Bean, 44
Bee, 92, 94
Bee-disease, Isle of Wight, 94
Bembex forcipata, 215
Bernhardi, 27
Biffen, Prof., 184
Bilharz, 145
Bilharzia worm, 136, 145, 146, 147, 148, 149
Bilharziasis, 91, 147, 148
Biology, science of, 71
Biometry, 67
Birds, 32, 37, 66, 84, 85, 86, 88, 89, 215
injurious, 88
of prey, 88
Birth-rate, control of, 59
Bitterling, 85
Bittern, 89
Blackhead, 85
Bladder-worm, 140
Blenny, 76, 77
Blood-worm, 90
Blumenbach, 112, 124
Bojanus, 144
Bonnet, Charles, 35, 103
Book-worms, 92
Boots, supposed effect of, 124, 125
Botany, 26, 31
systematic, 71
Bothriocephalus latus, 142
Bottomley, Prof., 93
Bourne, Prof., 19, 23, 79
Brachydactyly, 52
Bracken, 93

Brain, human, 120, 121, 122, 123, 126, 127
Breeding, science of, 5, 26, 29, 33, 34, 42, 54, 71, 157-188
experiments, 44, 49-53, 158-182
Bridges, 172
Browne, Sir Thomas, 103
Brown-tail moth, 87
Bruce, Lady, 218
Bruce, Sir D., 210, 218
Bubonic plague, 86, 137
Buchanan, R. M., 91
Buffon, 35, 106
Butler, 157
Butterflies, 37

Calandra granaria, 8
oryzae, 8
Calanus finmarchicus, 200
Calf, 142
Camouflage amongst lower animals, 16, 17, 69
Camper, 112
Carnivora, 115
Carp family, 74, 75
Carrageen, 191
Cassia goratensis, 215
Castle, Prof., 180
Cat, 84, 86
Catarrhini, 110, 118
Caterpillars, 37, 38, 85, 87
Cattle, 29, 42, 90, 91, 92, 141, 142, 143
Centipede, 84
Cercaria, 143, 144, 145, 146, 147, 148
Cereals, protection of stores, 6
Chalcidae, 10
Chalcidoidea, 216
Char, 72, 73
Chimpanzee, 103, 109, 112, 115, 117, 118, 120, 122, 127
Cholera, 91
Chondrus crispus, 191
Cichlidae, 74
Clonorchis sinensis, 145
Clothes moth, 92
Clupea sapidissima, 197
Clupeidae, 193
Cobbold, 145
Coccidia, 85
Cockles, 39, 195, 199
Cod, 193, 195, 196, 199, 203
Coelenterata, 105
Colonial Government, 218
Colonial Office, the, 218
Colour-blindness, 52
Competition, 27, 28, 38, 39, 40, 41, 42, 56, 58, 59
Continuity of germ-plasm, 47
Convergence, 110
Copaifera mopanie, 214, 215
Copepoda, 199, 200
Cormorant, 88
Correlation of organisms, 84
Crab, 88, 146
Crepidula, 39
Crops, 29, 85, 87
Crossochilus, 75
Crustacea, 93, 199
Cucullanus elegans, 150
Culex pipiens, 37
Cuvier, 124
Cyclops, 143, 150, 151
Cyprinidae, 74
Cythere, 39

Darwin, Charles, 27, 33-36, 37, 40, 42, 53, 57, 61, 68, 84, 95, 104, 110
Darwin, Erasmus, 18
Daubenton, 112
Dendy, Prof., 1, 65, 71, 79, 104
Diarrhoea, 91
Diatoms, 199, 200, 201
Diospyrus, 214
Diprotodon, 129
Distomum hepaticum, 92
Dog, 129, 130, 141, 152
Dog-fish, 203
Dog-whelk, 39
Doryphora, *see* Leptinotarsa
Dracunculus medinensis, 149
Dragon-fly, 87
Drosophila, 49, 50, 51, 53, 163, 166-169, 171, 182
Dubois, 106
Durrant, Mr. Hartley, 12
Dysentery, 91, 146

Earthworm, 84, 92
East Coast fever, 210
Ebony, 214
Echidna, 118
Economic Entomology, Bureau of, 69
Education, value of, 48

Eel, 88
Egret, 88
Elephantiasis, 90, 137, 149, 209
Embryology, 23
Entomology, 66
Eoanthropus, 128, 129, 130
Ephestia kuehniella, 12
Equality of nations and individuals, 28
Erythrina, 214
Ethnology, 101
Euproctis chrysorrhoea, 87
Eutheria, 129
Evolution, adaptive, 74, 75, 76, 77
  causes of, 70
  doctrine of, 95, 96
  "end-on," 104, 105, 107, 108
  progressive, 14, 15, 19-21, 30-34, 40, 56, 57, 96, 104, 107
  sequence of, 104, 105, 106
  vegetable, 31

Factors, 45, 46, 49, 51-54, 61, 161-171, 173-175, 177-182
Fannia canicularis, 91
Fasciola hepatica, 143
Fedschenko, 150
Feeble-mindedness, 52
Filaria bancrofti, 90
Filaria worms, 149
Fish, value as food, 191, 193, 194, 202
Fisheries, 13, 26, 70, 191, 192, 195-206
Fishery Board for Scotland, 197, 198
Fishes, economic importance of, 69, 70
  fresh-water, 88, 93, 142, 143, 146
  new species of, 68, 71
Flea, 86, 209
Flounder, 195, 196
Flour-moth, 12
Flukes, 143, 144, 145, 146, 147
Food, destroyers of, 6-12, 69, 85
  matters in the sea, 199, 200
  struggle for, 6, 33, 36
Foot, human, 124, 125, 126
Fruit-fly, *see* Drosophila
Fungi, 84, 92

Gadidae, 193
Galen, 111, 112
Galton, 35, 43, 46, 60
Gametes, 46, 47, 50, 157-182
Gametes, external influence on, 182
  purity of, 159, 160, 161, 162
Genetics, 29, 49, 157-188
Geographical distribution, 33
Geology, 66, 70
German point of view, 34
Germany, 27
Germ-cells, *see* Gametes
Germ-plasm, 45, 46, 47, 48, 51, 55
Giant creeper, 214
Gipsy-moth, 87
Glossina brevipalpis, 211
  fusca, 212
  longipennis, 211
  morsitans, 210, 211, 212, 213, 215, 217
  palpalis, 210, 211, 212, 213, 216, 217
Gnat, 37
Goodale, 173
Gorilla, 118, 122, 124, 126, 127
Government, the, 25, 26, 27
Grain-pests, damage, 6, 7, 8, 9, 10, 12
  remedial measures, 11
Grass, 214
Ground-ape, 127
Grouse, 88
Growth, 34
Grubs, 38
Guinea-pigs, 146
Guinea-worm, 136, 149, 150
Gyrinochilus, 75

Haddock, 193, 195, 196
Haeckel, 30, 105, 106, 107, 108, 109, 110, 113
Haematuria, 146
Hake, 193
Halibut, 195
Harris, Prof. Fraser, 86
Harvey, 34, 46, 47
Health Board, International, 154
Hedgehog, 92
Heracleitus, 31
Herdman, Prof., 13, 189
Heredity, 5, 14, 15, 34, 35, 42, 50, 54, 59, 60, 71, 157, 169, *see* Genetics
Heron, 88
Heros festae, 74
Herring, 191, 193, 194, 195, 196, 199, 200, 201, 202, 203
  family, 72, 74

Hippocrates, 137
Hookworm, 136, 149, 151, 152, 153, 154
Hornbills, 215
Horses, 90
House-fly, 90, 91, 209, 212
Howard, 184
Hubrecht, 127
Hydra, 105
Hymenoptera, 216

Ichneumon-fly, 92
Imperial College of Science, 79
Imperial Studies Committee, 3
Infantile paralysis, 91
Infusoria, 93
Inheritance of acquired structures, 47, 48, 49
Insectivora, 115
Insects, 38, 69, 86, 87, 88
Irrigation Department in Egypt, 148
Isolation, physical, 73

Jannsens, 167
Johannsen, 44, 47
Johnstone, Dr. J., 202
Jones, Prof. Wood, 20, 99

Kestrel, 88
Kidney, human, comparison with other Primates, 118
Kinghorn, Dr., 210, 218
King's College, 3, 93
Kingsley, Charles, 120
Knox, Robert, 103
Kuchenmeister, 140

Labour Party, the, 95
Lady-bird, 92
Lady-bug, 87
Laemophloeus, 9
Lagothrix, 122
Lamarck, 35
Lamborn, Dr., 216
Lamellibranchiate (Bivalve) molluscs, 38, 39
Lancashire Sea-Fisheries, 202, 204, 205, 206
Lankester, Sir Ray, 92
Lapwing, 92
Lawrence, Sir William, 112
League of Nations, 97
Leguminous plants, 92, 93
Leibnitz, 34
Leiper, Dr. R. T., 12, 91, 133
Lemur, 106, 107, 108, 110, 111, 115, 116, 118, 120, 126
Leprosy, 137
Leptinotarsa (Doryphora), 53, 86, 87
Lesser house-fly, 91
Leuckart, 141, 150, 152
Lice, 91, 209
Limnoca truncatula, 92
Ling, 193, 196
Linkage of factors, 164, 165
Linnaeus, 29, 102
Linnean Society, 35
Liverpool School of Tropical Medicine, 210
Liver-rot in sheep, 92
Lizard, 85, 86
Locke, 85
Looss, Prof., 152, 153
Lopholatilus chamaeleonticeps, 203
Lull, Prof., 87
Lyall, 30

Macaques, 122
Mackerel, 41, 195, 200, 202
Malaria, 13, 36, 37, 69, 90, 136, 151
Malthus, 38
Mammals, 32, 84, 105, 111, 115, 117, 119, 127, 130, 215
Man and animals, practical interrelation between, 92
  and the web of life, 85
  antiquity of, 126-131
  a parasite, 5
  Mendelian inheritance in, 52
  origin of, 20, 31, 101, 106-112, 115, 123-131
  primitiveness of, 113-127
  relation to Tarsius, 111, 118, 119, 126
  specialisation of, 120-127
  upright position of, 120, 123, 124, 125, 126, 127
  zoological position of, 30, 102, 103, 107-127
Manson, Sir Patrick, 137, 145, 209
Marmot, 86
Marsupials, 115, 129
May, Dr., 218
McConnell, 145
Medical entomology, 209
Melania, 145, 146

Mendel, Gregor, 35, 50, 157, 158, 160, 163, 185
Mendelian inheritance, 60, 157-182
Mendelism, 49
Metatheria, 116, 129
Militarism, abolition of, 28
Miller, Mr., 68
Minnows, 85
Mites, 10, 209
Mivart, 108, 109
Mole, 84
Mongoose, 85
Monkey, 103, 106, 107, 108, 110-120, 122-142, 126, 127, 146, 147, 150
Monostomum mutabile, 144
Moore, Prof. B., 200, 201
Morgan, Prof., 40, 49, 52, 53, 54, 58, 163, 166, 171, 174, 180, 182
Mosquito, 36, 37, 69, 70, 89, 90, 92, 149, 209
Moths, 37
Mouse, 52, 53, 54, 86, 89, 181, 182
Multiple factors, 179-181
Murray, Sir J., 201
Musca domestica, 91
Muscular system, human, comparison with other Primates, 115, 116, 117
Museums, centres of research, 65
  educational value of, 65
Mussel-culture, 204, 205, 206
Mussels, 39, 85, 195
Mutant, 53, 54, 55
Mutation, 53, 54, 61, 75
Mutillid, 216
Mycorhiza, 92

National Physical Laboratory, 79
Natural History Museum, 12, 25, 66, 69, 70, 77, 78, 79
Natural laws, 33, 34, 48
  selection, 33, 34, 38, 40-43, 48, 57, 95, 96, 131
"Nature," 79
Naunyn, 141
Neanderthal Man, 128, 130
Necator americanus, 151
Necrolemur, 111
Negro, 103
Nematoda, 149, 150, 151, 152, 153, 154
Newstead, Prof., 12, 207
Night-blindness, 52
Nilsson-Ehle, 177
Notharctus, 111

Oceanography, 199
Ocneria dispar, 87
Oken, 35
Ontogeny, 126
Ophthalmia, 91
Orang-utan, 106, 112, 118, 122
Ornithorhynchus, 117, 118
Owen, Sir Richard, 108, 109
Owl, 88
Oxyuris vermicularis, 138
Oyster, 39, 92, 195, 204

Palaeontology, 23, 101, 105, 109
Pangenesis, 34, 35
Paragonimus ringeri, 145
Parasites, human, 12, 13, 29, 36, 37, 90, 135-154
  migrations of, 140-146, 149-151
Parkia, 215
Pathology, 26
Pea, inheritance in, 50, 52, 157, 163, 164, 165, 166
Pearson, Prof. Karl, 60
Peat, agricultural values of, 93
Pecten, 39
Pellonula miodon, 74
Pelycodus, 111
Penguin, 123
Perch, 142, 150
Petroscirtes, 76, 77
Phascolomys, 118
Phlebotomus, 209
Phylogeny, 105-110, 126, 127, 129
Physiology, 67
Pig, 86, 141, 142, 149
Pike, 146
Pilchard, 193
Piltdown skull, 128
Pithecanthropus, 106
Pithecometra thesis, 106
Plaice, 193, 196-199, 203
Plato, 103
Platyrrhini, 110, 118
Pleuronectids, 41, 77, 193, 194
Plutarch, 136
Plymouth Marine Laboratory, 200
Pomace-fly, *see* Drosophila
Pork, 141, 149
Port Erin hatchery, 197, 198, 199, 200
Potato-beetle, 53, 55, 86, 87
Potato-plant, 86
Poultry, 85, 158-162, 169, 170, 173, 176-179
Predacity, 40

Preventive medicine, 26
Primates, 107, 108, 110, 115, 118, 121, 123, 126, 127, 130, 131
Privy Council for Scientific and Industrial Research, 78
Prototheria, 116
Punnett, Prof., 5, 93, 155

Quekett Microscopical Club, 71

Rabbit, 68, 85, 92, 181
Rat, 85, 86, 137, 146, 180
Rates of increase, 34, 41, 56
Recapitulation in development, 113, 121, 125
Reconstruction, social, 95
Red-buck, 90
Red flour-beetle, 9
Redia, 143, 144
Red-water, 91
Regan, Mr. Tate, 12, 63
Regression, law of, 43
Reproduction, 34, 42, 59
Reproductive system, human, comparison with other Primates, 118
Reptiles, 32, 84, 85, 105, 115, 116, 215
Research, 95, 105, 183, 218, 219
Reversion, 53, 115
Rhizopertha dominica, 8
Rhodeus amarus, 85
Rinderpest, 210
Rockefeller, Mr. J. D., 154
Rockefeller Sanitary Commission, 154
Round-worms, 149, 150, 151, 152, 153
Royal Society, the, 218
Rudolphi, 141
Ruffer, Sir Armand, 136

Salmon, 193
  family, 72
Sanya or Iron-wood tree, 214
Saw-toothed beetle, 9
Scale-insect, 87, 92
Scale of life, 103, 104, 105, 107, 108, 120, 127
Schistosoma, 91, 146
Seat-worm, 138
Sea-water, alkalinity of, 200
Secondary sexual characters, 172-175
Segregation, habitudinal, 73
Segregation, Mendel's law of, 53
Sex, experimental analysis of, 52, 167, 169-175
Shad, 72, 197
Sheep, 92, 141, 143
Shelley, 84
Shipley, Dr., 12
Siebold, 144
Silkworm, 92
Silvanus surinamensis, 9
Skull, human, comparison with other Primates, 112, 113, 114
Sleeping sickness, 13, 37, 90, 210, 216, 217, 218
  prevention of, 217, 218, 219
Smith, Allen J., 151
Smith, Dr. S. A., 129
Snails, fresh-water, 91, 144, 145, 146, 147, 148, 149
Snake, 85, 89, 92
Sole, 193
Somatoplasm, 47
Species, fixity of, 104
  origin of, 71, 72, 73, 74, 77
Spencer, Herbert, 34
Sphegidae, 38
Spider, 38
Spiny dog-fish, 203, 204
Spontaneous generation, 137, 140, 141
Sprat, 193, 202, 204
Sprengel, 83
Squirrel, 89, 215
Stable-fly, 91
Starfish, 39
Steenstrup, van, 143, 144, 145
Stegomyia fasciata, 90
Stirps, theory of, 46
Stomoxys calcitrans, 91
Strauss, 27
Strepsorrhini, 110
Struggle for existence, 4, 5, 13, 21, 27, 31, 32, 34, 38, 41, 42, 56, 95, 131
Sugar-beet, 43
Survival of the fittest, 27, 31, 40, 56, 131

Taenia solium, 141
Talgai man, 129, 130
Tapes, 39
Tapeworm, 137, 140, 141, 142
Tarsius, 110, 111, 118, 119, 120, 126, 127

Temora longicornis, 200
Termites, 84, 92, 214
Thomson, Prof., 81
Thylacoleo, 129
Tick, 91, 209
Tick-fever, 91
Tile-fish, 203
Tongue, human, comparison with other Primates, 117, 118
Top-minnows, 90
Tower, 53, 55
Trees, 84, 87, 92
Trematoda, 92, 143, 144, 145, 146
Treviranus, 35
Tribolium castaneum, 9
Trichina worm, 149
Trichinella spiralis, 86
Trichinosis, 86, 149
Trogoderma khapra, 9
Trout, 72, 87, 93
Trypanosoma gambiense, 216
 rhodesiense, 216
Trypanosome, 13, 90, 210, 216, 217
Trypanosomiasis, 216, 217
Tsetse-fly, 37, 90, 209-219
 breeding places of, 213, 214, 215
 general characters of, 210, 211
 life-cycle of, 211, 212, 213
Tuatara, 16
Turbot, 195, 196
Turkey, 92
Typhoid fever, 91
Typhus, 91
Tyson, Edward, 103, 112

Ungulates, 117
United States Bureau of Fisheries, 197, 202, 203, 204
Use and disuse, 34, 43

Variation, 34, 35, 42, 43, 44, 55, 104, 115, 131, 157
 quantitative, 175-181
Variegated plants, inheritance in, 182
Vascular system, human, comparison with other Primates, 117
Venus, 39
Versalius, 112
Vertebrates, origin of, 105
Vilmorin, Louis, 43
Vogt, Carl, 30
Vole, 88, 92
Vries, de, 35, 43

Wallace, 33, 35, 38, 42, 57
War, European, 26
 of nature, 34, 40
Wart-hog, 216
Wasp, 215
Waterflea, 143
Water wagtails, 92
Weasel, 88
Web of life, 83, 84, 90, 92, 93, 94, 95, 96, 97
Weevils, 7, 8, 9
Weismann, 30, 35, 38, 41, 61
Wells, H. G., 93
Whale, 92
White, Charles, 103
White, Gilbert, 83
White-ants, 84, 92, 214
Whitebait, 92
Whiting, 193
Wombat, 118
Wood-pigeon, 89
Worms, parasitic, 91, 135-143, 146 154

Xiphasia, 76, 77

Yellow fever, 90
Yorke, Dr. W., 210, 218

Zoology, definition of, 29
 economic, 11, 12, 13, 26, 28, 29, 69, 77
 educational and moral value of, 15-19, 28, 48, 56, 59, 60, 65, 77
 importance in social reconstruc tion, 27, 28, 29, 31, 48. 59, 60, 61
 philosophical, 67, 70, 77
 systematic, 67, 68, 70, 71, 73, 77

Printed in Great Britain by R. & R. Clark, Limited, *Edinburgh*.